THESIS

THE POLLINATION of some IMPORTANT AGRICULTURAL GRASSES with a view to Improved METHODS of BREEDING.

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(A general summary of the first two years work was read at the meeting of The Association of Economic Biologists, Edinburgh. February 1925; and a further contribution at a meeting of The Botanical Society of Edinburgh, March 1925.)

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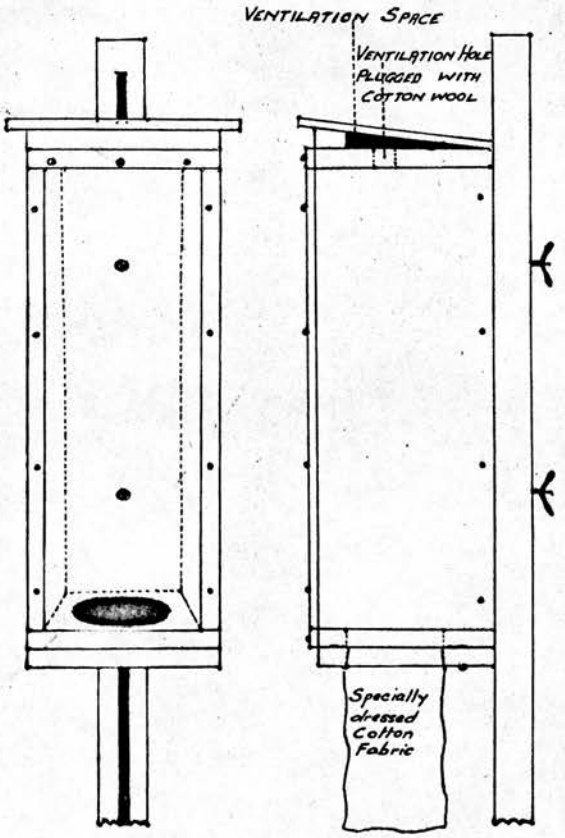
P.T.O.

POLLINATION of AGRICULTURAL GRASSES.

Work on the breeding of Agricultural grasses was started in 1922 at the Plant Breeding Station of the Scottish Society for Research in Plant Breeding. It was then found that little had been published on the methods of pollination in agricultural grasses, which in itself is the foundation of all future work on breeding. It is proposed to discuss here the pollination, both controlled and uncontrolled (natural), of the important agricultural grasses, and an attempt has been made to apply the results of these investigations to practical methods of breeding.

METHODS of ARTIFICIAL ISOLATION.

For experiments in controlled pollination it was first necessary to arrive at a method of artificial isolation, both reliable and practical. It was found that glazed semi-transparent (pergamine) paper bags gave good results both under glass and in the open, but owing to wind and rain in the latter position they became damaged and the results were unreliable. Fabric bags were experimented with in the field but these proved to be most unreliable. It was found on microscopical examination that, after exposure/



POLLEN-PROOF ISOLATION BOXES

exposure to wind and rain, the dressing had been removed from the spaces in the cloth, leaving holes, in many places, .3 mm. in diameter. On examination of the pollen of perennial rye-grass, it was ascertained that the grains were only .034 mm. in diameter. It was therefore necessary to find a method more suited to outdoor use. After various trials ventilated pollen proof boxes proved to be the best. These boxes had two decided advantages. Firstly, they were not liable to damage by weather and secondly, they were moveable vertically on the supporting stick, making adjustment for the increased growth of the plant easy.

It was necessary to make sure that the methods of isolation employed in no way retarded fertilisation. This point has, I think, definitely been proved, and will be discussed on page 90.

ENVIRONMENT.

Certain plants of the various species worked with were divided into three or more pieces in order to subject such plants to different conditions; in these cases one piece was kept in a large cool greenhouse, another piece in a small house heated throughout the winter, and the third in a plot outside. It was necessary to pot all grasses for inside work, and in so doing it was thought that abnormal results/

results might be obtained; but experiments carried out in the open showed no difference in the behaviour of pieces of an individual plant when potted and normally planted.

The following species were worked with:-

Italian Ryegrass (Lolium italicum; L.)
Perennial " (" perenne, L.)
Cocksfoot (Dactylis glomerata; L.)
Timothy (Phleum pratense; L.)
Alpine Timothy (Phleum alpinum; L.)
Tall Oat Grass (Arrhenatherum avenaceum, Beauv.)
Golden Oat Grass (Avena flavescens; L.)
Avena pubescens, Huds.
Various fescues.
Anthoxanthum Puellii, Lec. and Lam.
Meadow Foxtail (Alopecurus pratensis; L.)

Notes were also made on the following:-

Avena fatua, L.
Avena pratensis, L.
Poa annua, L.
Alopecurus geniculatus, L.

ITALIAN RYEGRASS.

ORDER OF FLOWERING.

(a)/

(a) SPIKE and (b) SPIKELET.

(a) SPIKE: Flowering proceeds in a more or less regular manner from the apex downwards.

(b) SPIKELET: The basal flowers reach maturity first and flowering continues extremely regularly upwards.

The following table gives the times at which each flower of the terminal spikelet of a spike, and also those of the lowest spikelet, opened in a typical case.

TABLE I.

PLANT	DATE	TIME	FLOWER
Cd_2 (4)	21/6	2.25	1 opening
Spikelet 1	22/6		No flowers on any plant opened to-day.
	23/6	11.50	2 opening
	24/6		3 flowered
	25/6	11.59	4 opening
	26/6	1.20	5 opening
	27/6	1.15	6 opening
Cd_2 (4)	23/6	11.25	1 opening
	24/6		2 and 3 flowered
Spikelet 12	25/6	11.30	4 opening
		1.30	5 opening
	26/6	1.25	6 opening
	27/6	1.30	7 opening
	28/6	4.30	8 opening
	29/6	11.35	9 opening

NOTE: The basal flower of the spikelet is No.1.

N.B. Throughout this paper SUMMER time is used.

OPENING/

OPENING of FLOWERS.

At the time the flowering glume and pale separate the filaments of the stamens are still short, but elongation then rapidly takes place, and when almost full grown the anthers fall over and take up a position below the laterally projecting stigmas. Dehiscence takes place, generally, shortly after the filaments are fully developed, but may be delayed for some time after. In no case were the anthers observed to dehisce before the opening of the flower.

Table II. shows the time taken between the opening of the flowers and dehiscence of the Anthers in plant Cd_2 (4), which is typical of the many plants under observation. On examination of exposed stigmas, before the dehiscence of their respective anthers, they were often found to be covered with pollen either from flowers on the same plant or from neighbouring plants. It has been found by experiment that the stigmas, at this time, are receptive, therefore under natural conditions, even if Italian Ryegrass were self-fertile, cross pollination would be common.

TABLE II./

TABLE II.

9th. JUNE Cd_2 (4)			11th. JUNE		
a.m.		INTERVAL between OPENING & DEHISCENCE Minutes	a.m.		INTERVAL between OPENING & DEHISCENCE Minutes
11.34	Flower opening	2	10.34	Flower opening	10
11.36	Anthers dehisced		10.44	Anthers dehisced	
11.34	Flower opening	3½	10.43	Flower opening	27
11.37½	Anthers dehisced		11.10	Anthers dehisced	
11.35½	Flower opening	3	11.29	Flower opening	9
11.38½	Anthers dehisced		11.38	Anthers dehisced	
11.36	Flower opening	2	11.28½	Flower opening	9½
11.38	Anthers dehisced		11.38	Anthers dehisced	

It will be seen from the table that the period between opening of the flowers and dehiscence varied considerably. This variation appears to be due chiefly to the difference in atmospheric conditions which obtained during the two days the plants were under observation, as in both cases the flowers were/

were on the same plant. Differences in the times do occur, however, when two or more flowers on a given plant open at the same time. One instance is shown in the above table. The maximum morning temperature of the 9th and 11th was almost the same, 82°F and 80°F respectively, but the 11th being a Monday the greenhouse was appreciably dryer than on the 9th, the house not having been watered on the 10th. This may partly account for the late dehiscence on the 11th.

The longest period observed on any day between the opening of flowers and dehiscence of their anthers was 4 hours 45 minutes.

CLOSING of FLOWERS.

Generally the flowers remain open for about three hours. The average time for 81 flowers of plant Cd_2 (1) was 2 hours 50 minutes. These were not all observed on the same day, but spread over a period of about 3 weeks. There were exceptional cases where flowers remained open for a day or more; but these will be discussed later.

DAILY FLOWERING PERIOD. (Cool greenhouse conditions)

This varies to a certain extent. On the majority of days the first flowers opened between 11 a.m. and 12 noon. In a few cases flowering took place early in the forenoon or was delayed till the afternoon/

afternoon. On no day did flowering commence before 9.30 a.m.

After the first flowers of the day have opened, flowering continues rapidly for an hour or so, after which time occasional flowers open till about 5 p.m., when flowering as a rule stops for the day.

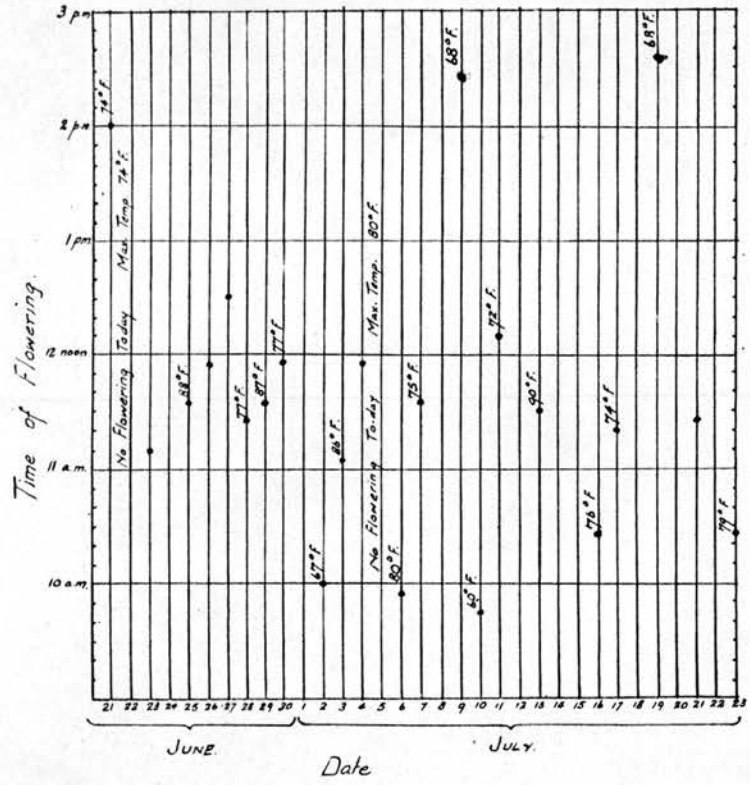
Atmospheric conditions appear to regulate, to a certain extent at least, the time at which the first flowers open.

The temperature obtaining on a given day is certainly not the only regulating factor for that day, for on some days flowering began early at a comparatively low temperature (see Table III.). For example, the 22nd of June was dull with a maximum temperature of 74°F. On this day no flowers on any plant opened. Yet on the 10th of July flowering commenced exceptionally early at a temperature of 60°F. This may be owing to the presence of moisture in the atmosphere, rain having fallen since early morning.

TABLE III./

TABLE III.

Note : Temperature at which flowering commenced is given in most cases.



TIME TAKEN BY SPIKES TO COMPLETE FLOWERING.

Under greenhouse (cool) conditions an average spike takes less than 14 days to flower. Typical examples are given in Table V.

TABLE/

TABLE V.

PLANT	No. of SPIKELETS	No. of FLOWERS	DATE when 1st FLOWER opened	DATE when last FLOWER opened	No. of DAYS
$Cd_2(1)$	21	123	10/6	20/6	11
"	19	105	13/6	23/6	11
"	25	142	11/6	22/6	12
$Cd_2(4)$	12	91	21/6	29/6	9

SELF-POLLINATION.

In the following experiments most work was done with seedlings (identification mark Cd_2) taken from a strain, whose individuals varied slightly in many respects, e.g., type of spike, colour of basal leaf sheaths, and, as was discovered later, also in length of life.

Five plants were divided into several pieces and potted. A certain number of all five groups were planted in a small house which was heated during the winter only, several in a large cool house, and the remainder in the open; a few of the latter were planted, the rest being kept in pots. These last acted as controls which proved that potting had no detrimental influence on seed production.

In all cases of controlled pollination glazed/

glazed paper bags and pollen proof boxes were employed. It was thought at first advisable when selfing flowers to apply the pollen by hand, but later it was found that autonomous self pollination was equally satisfactory, for on examination of the stigmas ample pollen was observed on them.

The following table shows the results of self-pollination:-

TABLE VI.

SELF-POLLINATION

PLANT	DATE of BAGGING	No. of SPIKES	No. of FLOWERS	No. of SEEDS	% Fls. SETTING SEED	REMARKS
Cd_2(1	3/6	2	302	0	0	L.H 1925
"	12/6	1	96	0	0	L.H 1924
"	14/6	1	95	0	0	L.H 1924
"	14/6	1	101	1	1	L.H 1925*
"	16/6	3	710	0	0	L.H "
"	16/6	1	234	0	0	L.H "
"	18/6	1	53	0	0	S.H 1924
"	18/6	1	55	0	0	S.H. "
"	24/6	1	119	1	.8	0 1924
"	13/7	1	136	0	0	0 1923
"	13/7	1	135	0	0	0 "
"	8/8	1	91	0	0	L.H "
"	8/8	1	87	0	0	L.H "
"	8/8	1	106	1	.9	S.H "
"	8/8	1	98	0	0	S.H. "
"	13/8	1	71	0	0	S.H "
"	14/8	1	102	0	0	L.H "
"	14/8	1	102	1	.9	L.H "
"	14/8	1	126	0	0	L.H "

NOTE: L.H. = Cool House
S.H. = Small House heated during winter
0 = Outside
* = Self pollinated by hand

TABLE VI. (cont.)

PLANT	DATE of BAGGING	No. of SPIKES	No. of FLOWERS	No. of SEEDS	% Fls. SETTING SEED	RE-MARKS
$Cd_2(2)$	18/6	1	126	0	0	L.H.1924
"	18/6	1	93	1	1.1	L.H "
"	24/6	1	173	0	0	0 "
"	28/6	1	104	0	0	0 "
"	3/7	2	242	0	0	L.H.1923
"	3/7	1	38	0	0	L.H. "
"	3/7	2	329	1	.3	L.H. "
"	13/7	1	162	1	.6	0 "
"	13/7	1	72	0	0	S.H. "
$Cd_2(3)$	14/6	1	62	0	0	S.H.1924
"	16/6	1	134	0	0	L.H.1925
"	16/6	5	514	5	1.	L.H. "
"	21/6	1	51	0	0	L.H.1924
"	3/7	1	134	0	0	L.H.1923
"	21/7	1	24	0	0	L.H.1925*
"	8/8	1	51	0	0	L.H.1923
"	8/8	1	86	0	0	L.H. "
"	8/8	2	223	0	0	L.H. "
"	8/8	1	69	0	0	S.H."
"	8/8	1	71	0	0	S.H. "
"	14/8	1	61	1	1.6	L.H. "
"	14/8	1	96	0	0	L.H. "
$Cd_2(4)$	26/5	1	126	0	0	L.H.1925
"	26/5	5	651	6	.9	L.H. "
"	29/5	2	254	0	0	L.H. "
"	5/6	1	84	0	0	S.H.1924
"	6/6	1	172	0	0	L.H. "
"	6/6	1	182	0	0	L.H. "
"	22/6	2	342	0	0	L.H.1923
"	7/7	2	308	0	0	L.H. "
"	7/7	1	162	0	0	S.H.1923
"	9/7	1	140	1	.7	L.H. "
"	14/8	1	93	0	0	S.H. "
"	14/8	1	87	0	0	S.H. "
"	14/8	1	76	0	0	S.H. "
$Cd_2(5)$	11/6	1	223	1	.4	L.H.1924
"	16/6	1	184	1	.5	L.H.1925
"	16/6	2	405	2	.5	L.H. "
"	24/6	1	216	4	1.9	L.H.1924
"	2/7	2	252	3	1.1	L.H.1923
"	13/7	1	189	0	0	0 "
"	8/8	1	105	0	0	L.H. "
"	14/8	2	132	0	0	L.H. "

It will be seen from the table that all five plants were almost completely self-sterile. There is no evidence of mid or end season fertility as observed by Professor Montagu Drummond (observations on Lathyrus species) and others.

The influence of different environment in no way increased self-fertility; neither was there any definite increase in the self-fertility percentage when more than one spike was enclosed in a bag.

Other 17 plants of Italian Ryegrass were selfed (in addition to those already mentioned). The percentage of flowers setting seed ranged from 0% to 15% in a single instance; this latter percentage appears to have been an error, as this plant on repeated selfing later never reached more than 5.5%. The highest reliable figure was 7.6%, 73% of which germinated when sown.

CROSS FERTILITY.

Hand crosses were made between the 5 plants of strain Cd_2, and from the results it was ascertained that all 5 plants were completely cross-fertile.

In order to test the possibilities of crossing self-sterile plants on a large scale and at the same time obtain additional proof of the efficiency of the/

the methods of isolation, spikes from different plants were enclosed together. It was necessary to have a standard of fertility with which to compare the results of the controlled crosses. This standard was taken as the maximum percentage obtained when the plants (with normal, i.e. uncut spikes) were freely exposed among themselves and with other plants of Italian Ryegrass outside. Some of the results of the controlled crossings very nearly approached this standard (see Table VII). When the same cross was repeated several times the results varied considerably owing to (1) one spike flowering before the other,

(2) one spike being taller than the other,

in which case the tall spike produced few seeds.

TABLE VII.

CROSS POLLINATION.

CROSS	PARENTS	No.of SPIKES	No.of FLS.	No.of SEEDS	% Fls. SETTING SEED
$Cd_2(1)$ X $Cd_2(2)$	$Cd_2(1)$	1	106	71	67
	$Cd_2(2)$	1	127	87	68
$Cd_2(2)$ x $Cd_2(5)$	$Cd_2(2)$	1	122	89	73
	$Cd_2(5)$	1	203	135	66
STANDARD					

$Cd_2(1)$ = 73%

$Cd_2(2)$ = 79%

NATURAL SEEDING.

These 5 plants of the population Cd_2 were very well adapted to experiments on natural pollination, all being mutually cross-fertile.

TABLE VIII.

NATURAL SEEDING IN GREENHOUSE.

PLANT	No.of SPIKES	No.of FLS.	No.of SEEDS	%	DATE of COMMENCEMENT of FLOWERING
$Cd_2(1)$	1	121	4	3.3	) All these
	1	135	6	4.4	) Spikes star-
	1	136	7	5.1	) ted flower-
	1	162	9	5.5	) ing within a
	1	135	10	7.4	) few days of
	1	142	11	7.7	) the 15/6.
	1	87	53	60.9	12/7
	1	59	35	59.3	18/7
	1	66	34	51.5	18/7

NOTE: This plant was in the Small House.

Table VIII. shows the effect on seed production of an increase in the pollen supply. The small percentage of seeds produced by spikes starting flowering about 15th June can be accounted for as follows. Up to 21st June $Cd_2(1)$ was the only plant of Italian Ryegrass in the house, with the exception of $Cd_2(4)$ which was not in close contact with it. On the 21st June several plants of Italian Ryegrass were brought in, but did not commence flowering for a considerable time/

time after entrance. During July the house was constantly filled with Italian Ryegrasses in flower, thus the great increase in seed production.

The variations are due in this case to the amount of foreign pollen available during the time the stigmas were receptive and not to a mid-seasonal increase in fertility, as was proved by hand-crossing at intervals throughout the flowering season. This point is extremely important from the point of view of isolation of strains as will be discussed later.

Similar results to the above were obtained outside. It was found that in spikes which were flowering about one date the percentages of Natural Seed set were more or less uniform.

EMASCULATION.

The most suitable time was found to be when the spike had almost totally emerged from the "shot blade". All flowers in the spikelet, except the two lowest were removed. At this stage with ordinary care the anthers may easily be removed entire, without damage to the stigma. The upper of the two flowers left on the spikelet was emasculated first (when this method is followed there is little chance of leaving a flower unemasculated). The lowest flowers on the spike/

spike may be emasculated later when fully clear of the "shot blade" or may be removed. For the operation forceps with fine blades and rounded points were used.

Diagrams of the spikes intended to be used for experimental purposes were drawn in a note book and each flower received a number. In this way it was possible to keep an exact note of the behaviour of the different flowers. At the time of emasculation when removing the stamens from a flower, the danger of that flower being fertilised with pollen from its own stamens is remote, although the stigma at the time is receptive, since the pollen is immature and non-functional. There is, however, a considerable risk of fertilisation by mature foreign pollen alighting on the stigma during the operation, and to obviate this it is advisable to emasculate in the morning before the day's flowering has commenced, and also to make the house as draught proof as possible.

TIME DURING WHICH THE STIGMA IS RECEPTIVE.

For the determination of the time during which the stigmas are receptive it was necessary to know the length of time the pollen to be applied to the stigmas would remain viable after dehiscence (as otherwise/

otherwise fresh pollen might remain on a stigma which had not yet become receptive and effect fertilisation after several days). This was done for the five plants of Cd_2. In no case did fertilisation follow pollination with pollen which had been kept for 24 hours after dehiscence.

Some experiments were carried out, in which pollen was applied to stigmas at the time of emasculation and various times after up to 118 hours after the opening of the flowers, in order to determine the most suitable time for pollination.

POLLINATION AT TIME OF EMASCULATION (approx. 4 days before flowers open)

I. 21/7/23. 11.10 a.m.

15 spikelets of $Cd_2(3)$ were emasculated (all flowers removed except two per spikelet).

The upper 15 flowers were pollinated with "fresh" pollen from plant $Cd_2(4)$.

The lower 15 wi th fresh pollen from plant $Cd_2(5)$.

The spike was bagged immediately after pollination.

The bags were not removed till the seeds were counted.

Result:-

Upper 15 flowers set 4 seeds.

Lower 15 flowers set 4 seeds

= 27%.

II. 21/7/23. 11.45 a.m.

12 spikelets of a spike on plant $Cd_2(3)$ were emasculated (all flowers removed except 2 per spikelet).

(a) A spike of $Cd_2(4)$, at a similar stage of development as the emasculated spike of $Cd_2(3)$ was selected. From this the anthers from the 2 lowest flowers on each of the first 4 spikelets were removed. Broken pieces of these anthers were inserted between the pales and the flowering glumes of the corresponding flowers on the emasculated spike of $Cd_2(3)$.

Result:- No seeds.

(b) The 8 flowers on the 4 spikelets immediately below those in (a) were pollinated with pollen from freshly dehisced anthers of $Cd_2(4)$.

Result:- 3 seeds = 38%.

(c) The 8 flowers on the lowest four spikelets had their anthers removed. Broken pieces of these anthers were replaced.

Result:- No seeds.

Experiments/

Experiments I. and II.(b) show that, at the time of emasculation (approx. 4 days before flowering) when pollen from freshly dehisced anthers of a plant of Italian Ryegrass was applied to the stigmas of a cross-fertile plant a certain proportion of flowers set seed. The time the pollen used in these crosses remained viable after the dehiscence of the anthers was known to be not longer than 24 hours. It is obvious, therefore, that certain stigmas were either receptive at the time of pollination or became so within 24 hours. This fact necessitates precautions being taken to prevent the contamination of stigmas by foreign pollen at the time of emasculation.

In order to test the possibility of self-pollination as a result of damaged anthers at the time of emasculation, flowers were self-pollinated at the time of emasculation.

II.(c). As was expected, no seeds were obtained since this plant had previously proved to be almost completely self-sterile. In experiment II(a), in order to overcome this self-sterility difficulty, immature pollen from another plant of Cd_2 at a corresponding age to the stigmas of $Cd_2(3)$ was used, with the same result; showing that at the time of emasculation/

TABLE IX — PERIOD DURING WHICH STIGMAS ARE RECEPTIVE (Cd_2 (1) ♀ ; Cd_2 (4) ♂)

Spikelet No.	Flower No.	July 2nd a.m. 10.30	July 2nd a.m. 11.40	July 2nd p.m. 2.45	July 2nd p.m. 4.40	July 3rd a.m. 11.20	July 3rd p.m. 2.45	July 3rd p.m. 4.45	July 4th noon 12	July 4th p.m. 4.	July 5th a.m. 10.30	July 5th p.m. 3.	July 6th a.m. 9.50	July 6th p.m. 4.	July 7th a.m. 11.45	July 9th p.m. 1.55	Seed Set.	Pollination.
I	1	OGX	O	C	CG	C	C	C	C	C	C	C	C	C	C	C	Seed	Opening.
	2			OX	O	C	C	C	C	C	C	C	C	C	C	C	"	Open *
II	1					OX	C	C	C	C	C	C	C	C	C	C	"	"
	2					OX	C	C	C	C	C	C	C	C	C	C	"	"
III	1				O	OX	C	C	C	C	C	C	C	C	C	C	"	18 hr. 40 m. after Opening.
	2					OX	50	50	C	C	C	C	C	C	C	C	Lost	—
IV	1							O	50	50	50	50	50X	50	C	C	Seed	65 hr. 5 m. after Opening.
	2							O	C	C	C	C	VSOX	VSO	C	C	"	65 hr. 5 m. " "
V	1					FW&CX	C	C	C	C	C	C	C	C	C	C	"	Flowered & Closed.
	2					OX	O	C	C	C	C	C	C	C	C	C	"	Open
VI	1					OX	C	C	C	C	C	C	C	C	C	C	"	"
	2					OX	O	VSO	C	C	C	C	C	C	C	C	"	"
VII	1			OX		C	C	C	C	C	C	C	C	C	C	C	"	"
	2					NOT			OBSERVED				OPENING				No Seed	Not Pollinated.
VIII	1					NOT			OBSERVED				OPENING				"	" "
	2					OX	O	C	C	C	C	C	C	C	C	C	Seed	Open
IX	1					OX	O	VSO	C	C	C	C	C	C	C	C	"	"
	2											VSO	50X	½O	VSOX	C	"	16 h. 50 m ? after Opening
X	1					OGX	O	C	C	C	C	C	C	C	C	C	"	Opening
	2													O	VSOX	C	No Seed	19 h. 5 m. after Opening
XI	1					OGX	O	C	C	C	C	C	C	C	C	C	Seed	Opening
	2							O	50X	50	50	50	C	C	C	C	No Seed	19 hr. 15 m. after Opening
XII	1					OGX	O	C	C	C	C	C	C	C	C	C	Seed	Opening
	2							O	C	C	C	C	VSO	½O	50X	C	"	90 hrs 20 m. after Opening
XIII	1							O	150X	C	C	C	C	C	C	C	"	19 hrs 15 m " "
	2								OGX	O	VSO	VSO	C	C	C	C	"	Opening
XIV	1								OX	O	C	C	C	C	C	C	"	Open
	2										½OX	C	C	C	C	C	"	"
XV	1								OX	O	C	C	C	C	C	C	"	"
	2								OGX	O	½O	50	50	VSO	C	C	No Seed	Opening
XVI	1								OGX	O	C	C	C	C	C	C	Seed	"
	2					NOT			OBSERVED				OPENING				No Seed	Not Pollinated.
XVII	1								OGX	O	C	C	C	C	C	C	Seed	Opening
	2								OX	O	C	C	C	C	C	C	"	Open
XVIII	1											VSO	VSOX	C	C	C	"	16 hrs 50 m. after Opening
	2					NOT			OBSERVED				OPENING					Not Pollinated
XIX	1											50	C	C	C	C	No Seed	" "
	2											O	CX	C	C	C	Seed	16 hrs 50 m. after Opening.

OG = Opening
O = Open
½O = ½ Open
50 = Slightly Open
VSO = Very Slightly Open
C = Closed
X = Crossed Cd_2 (4).
* Open means pollinated immediately on opening.

21 (a)

emasculation the pollen is not sufficiently mature to function.

POLLINATION AT TIME OF OPENING AND LATER.

For these experiments pieces of plant $Cd_2(1)$ were used as female parents. These were emasculated early, bagged, and placed in a house where no other ryegrasses were permitted to flower. Pollen was obtained from other plants of Cd_2 in another house. Several control spikes on pieces of plant $Cd_2(1)$ (female parents) were emasculated and left uncovered. None of these set a seed, affording a proof of the complete isolation under which the plants were kept.

A few of the results are seen in Table IX. In this table the Roman figures on the left represent the number of the spikelet on the spike, the terminal spikelet being I.

All flowers on each spikelet were removed except the basal one and that immediately above it. The basal flower on each spikelet is denoted by 1, the one above it by 2.

The dates and times are given at the top of each column.

Table X. shows in detail the result of delayed pollination and of non-pollination on the behaviour of/

TABLE X.

SPIKELETS XII – XVIII $Cd_2(1)\,♀ \times Cd_2(4)\,♂$

SPIKELET No.	FLOWER No.	July 4 p.m. 4·15	July 5 a.m. 10·45	July 5 p.m. 5·10	July 6 a.m. 10·30	July 6 p.m. 4.	July 7 a.m. 11·20	July 9 p.m. 2·5	July 10 a.m. 11·15	July 12 p.m. 5.	July 13 p.m. 4.	July 14 a.m. 11.	July 16 a.m. 11·10	July 17 p.m. 4·30	July 18 p.m. 2	July 19 a.m. 11·45	July 20 p.m. 2.	July 23 p.m. 2.	SEEDS SET	POLLINATION.
XII	1			SO	O	C	C	C × $Cd_2(4)$	C	C	C	C	C	C	C	C	C	C	No Seed	93 h. 5 m. after OPENING
	2			SO	VSO	SO	½ O	O "	½ O	C	C	C	C	C	C	C	C	O	Seed	" "
XIII	1		SO	SO	SO	SO	SO	¼ O "	SO	SO	VSO	C	C	C	C	C	O	C	No Seed	99 h. 20 m. "
	2	O	SO	VSO	SO	VSO	VSO	SO "	VSO	C	C	C	C	C	C	C	O	C	Seed	118 h. 10 m "
XIV	1	O	C	C	VSO	VSO	SO	VSO "	VSO	C	C	C	C	C	C	C	C	C	No Seed	" "
	2			O	VSO	VSO	SO	½ O "	VSO	C	C	C	C	C	C	C	C	C	Seed	93 h. 5 m "
XV	1	O	SO	SO	SO	SO	SO	½ O "	¼ O	C	C	C	C	C	C	C	C	C	No Seed	118 h. 10 m "
	2			O	VSO	VSO	SO	½ O "	¼ O	C	C	C	C	C	C	C	C	C	"	93 h. 5 m "
XVI	1	O	VSO	VSO	SO	¼ O	SO	SO "	VSO	C	C	C	C	C	C	C	C	C	"	118 h. 10 m "
	2					NOT			OBSERVED						OPENING					—
XVII	1		SO	VSO	½ O	½ O	½ O	½ O "	SO	C	C	C	C	C	C	C	O	C	"	99 h. 20 m. "
	2			O	½ O	½ O	½ O	½ O "	½ O	½ O	¼ O	SO	SO	VSO	VSO	VSO	VSO	C	"	93 h. 5 m "
XVIII	1	O	VSO	C	VSO	SO	SO	½ O "	SO	SO	SO	SO	VSO	C	C	C	C	C	"	118 h. 10 m "
	2					NOT			OBSERVED						OPENING					

SPIKELETS I – XI $Cd_2(1)\,♀$ – NOT POLLINATED

SPIKELET No.	FLOWER No.	July 3 a.m. 11·30.																	
I	1	Fld. C	VSO	SO	SO	SO	SO	SO	VSO	VSO	C	C	C	C	C	C	C	C	C	—
	2	Fld. SO	O	½ O	O	O	O	O	¼ O	SO	VSO	VSO	C	C	C	C	C	C	C	—
II	1	O	VSO	¼ O	SO	O	SO	O	SO	SO	C	C	C	C	C	C	C	C	C	—
	2	O	C	¼ O	O	O	O	O	O	½ O	¼ O	SO	SO	SO	SO	SO	VSO	C	C	—
III	1						SO	C	C	C	C	C	C	C	C	C	C	C	C	—
	2	O	SO	O	O	O	O	O	½ O	½ O	SO	SO	SO	SO	VSO	VSO	C	C	C	—
IV	1	O	C	VSO	SO	SO	SO	SO	SO	VSO	C	C	C	C	C	C	C	C	C	—
	2	O	C	VSO	SO	SO	SO	SO	SO	VSO	C	C	C	C	C	C	C	C	C	—
V	1	Fld. VSO	O	O	O	O	O	O	SO	VSO	C	C	C	C	C	C	C	C	C	—
	2						O	C	C	C	C	C	C	C	C	C	C	C	C	—
VI	1	O	SO	SO	O	½ O	½ O	½ O	¼ O	¼ O	¼ O	SO	VSO	C	C	C	C	C	C	—
	2	O	VSO	SO	O	½ O	½ O	½ O	¼ O	¼ O	SO	VSO	VSO	C	C	C	C	C	C	—
VII	1	O	VSO	SO	½ O	½ O	½ O	½ O	½ O	¼ O	SO	SO	VSO	C	C	C	C	C	C	—
	2	O	VSO	SO	½ O	½ O	½ O	½ O	½ O	¼ O	SO	VSO	VSO	C	C	C	C	C	C	—
VIII	1	O	VSO	SO	½ O	½ O	½ O	½ O	½ O	¼ O	SO	SO	VSO	C	C	C	C	C	C	—
	2	O	VSO	SO	½ O	½ O	½ O	½ O	½ O	¼ O	SO	VSO	C	C	C	C	C	C	C	—
IX	1					VSO	½ O	C	C	C	C	C	C	C	C	C	C	C	C	—
	2	O	C	SO	SO	SO	½ O	½ O	¼ O	¼ O	¼ O	SO	VSO	VSO	VSO	C	C	C	C	—
X	1	O	VSO	SO	½ O	½ O	¼ O	½ O	VSO	VSO	C	C	C	C	C	C	C	C	C	—
	2		VSO	SO	½ O	½ O	½ O	½ O	½ O	½ O	¼ O	SO	SO	VSO	VSO	VSO	VSO	VSO	VSO	—
XI	1						O	C	C	C	C	C	C	C	C	C	C	C	C	—
	2							C	C	C	C	C	C	C	C	C	C	C	C	—

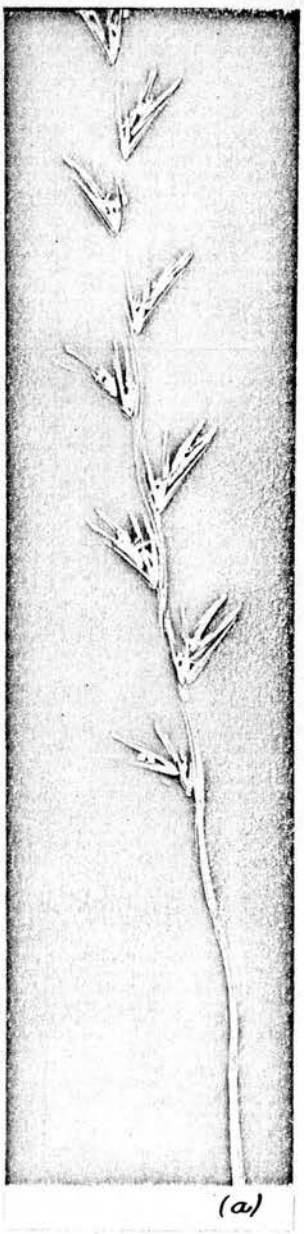
O = Open.
½ O = ½ Open
¼ O = ¼ Open
SO = Slightly Open
VSO = Very Slightly Open
C = Closed
Fld. C = Flowered & Closed.

of the flowers. A spike of Cd_2(1) was emasculated; as before, all flowers except the two lowest on each spikelet were removed.

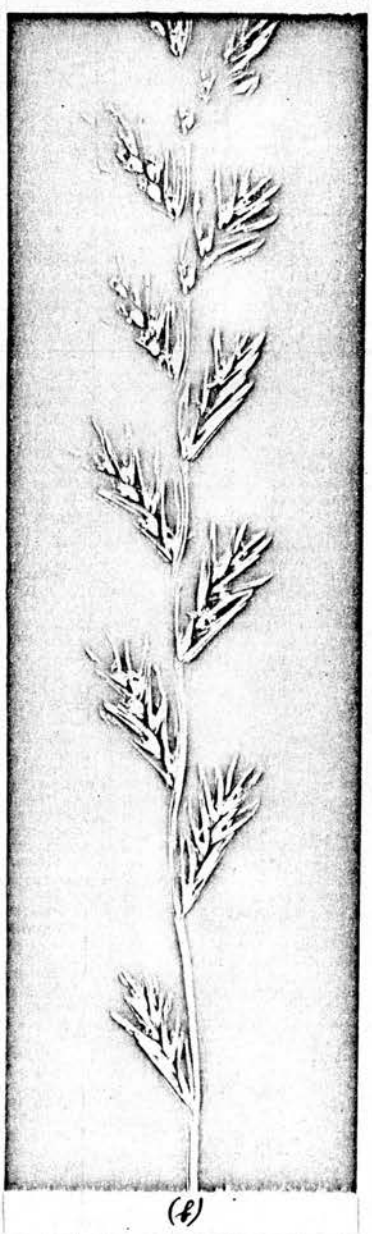
The upper eleven spikelets were not pollinated. The remainder (XII-XVIII) were cross-pollinated several days after the opening of the flowers. The longest interval between the opening of a flower and pollination, and where seed resulted, was 118 hours.

It would appear from Table X. that the fact of pollination, with pollen from a cross fertile plant not necessarily resulting in fertilisation, has some influence on the flowers causing them to close more rapidly than flowers where pollination was omitted. If Tables IX. and X. are compared, the difference in behaviour between flowers pollinated at the time of opening or shortly after, and those where pollination was delayed for several days, is distinctly seen. In the first case where fertilisation takes place, the flowers close after a few hours, the glumes never again opening, but in the latter the flowers may close as in the first example, and then after a certain time has elapsed reopen or partially reopen, and remain thus for several days; during the early part at least/

The photographs show open flowers, on two spikes of Lolium perenne, several days after pollination.
Spike (a) - Stigmas pollinated with "stale" Perennial Ryegrass pollen. - No fertilisation.
Spike (b) - Self pollinated - No fertilisation.



(a)

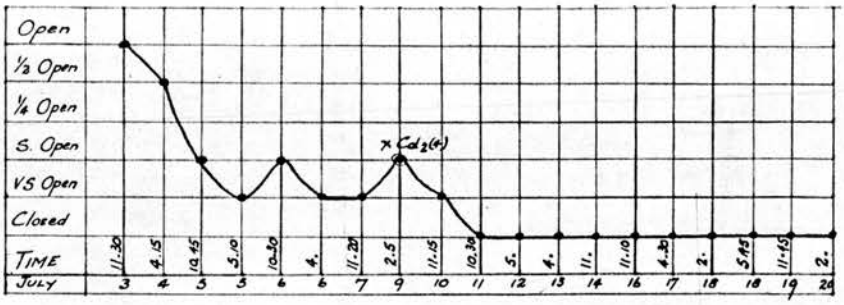


(b)

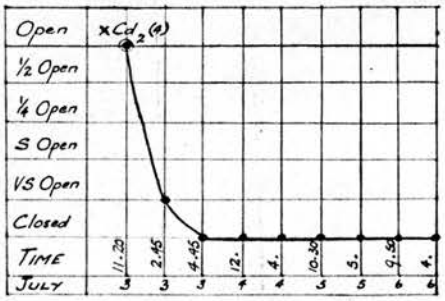
TABLE XI

(a) NOT POLLINATED

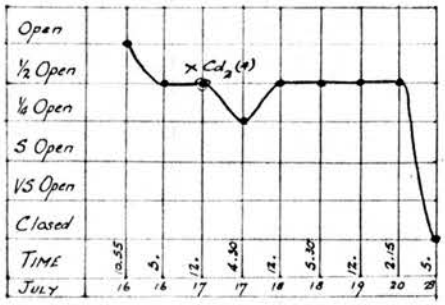
(b) DELAYED POLLINATION



(c) POLLINATION FOLLOWED BY FERTILISATION



(d) POLLINATION NOT FOLLOWED BY FERTILISATION



least of this second opening the majority of stigmas are still receptive.

The difference in behaviour between early, late and non-pollinated flowers are perhaps more clearly demonstrated in Tables XI.(a), (b) and (c).

Table XI(c) shows the typical behaviour of flowers pollinated at the time of opening when followed by fertilisation. The rapidity with which the flowers close after pollination will be readily seen.

Table XI(d) is typical of flowers which are pollinated and where fertilisation does not occur. In this case "stale" pollen (24 hours old) was employed with the result that no seeds were produced.

POLLEN.

Some experiments were carried out in order to determine at what stage of development pollen could most profitably be applied to the stigmas, and also for what period pollen remains viable after dehiscence of the anthers.

As regards the first point, it was ascertained that, when stigmas were pollinated with pollen from flowers which had not opened, i.e. with immature pollen, no seeds resulted. Pollen from freshly dehisced anthers gave the best results.

In/

In experiments on the time that pollen remains viable after dehiscence many flowers were pollinated with 24 and 48 hours old pollen (i.e. pollen ex anthers which had dehisced 24 and 48 hours previously) which was kept in cotton wool stoppered specimen tubes in the dark. In no case did any flower pollinated with such pollen set seed. If these findings are general for all Italian Ryegrasses, it is most unfortunate from the practical point of view, as it is often difficult to collect fresh pollen when required.

PERENNIAL RYEGRASS.

ORDER OF FLOWERING.

Similar to that described for Italian Ryegrass.

OPENING OF FLOWERS.

As in Italian Ryegrass, there is always an interval between the opening of the flowers and the dehiscence of their anthers. Variations in this interval occur.

There is a certain amount of evidence that differences in the period between opening and dehiscence are due to differences in the constitution of individual/

individual plants as the interval is fairly constant for flowers on the same plant which open at the same time.

The shortest time observed for any plant was two minutes, and the longest 1 hour 17 minutes. On the average the interval was slightly longer than was the case in Italian Ryegrass.

In one or two plants the filaments of the stamens, instead of developing normally, remained short, the result being that instead of the anthers hanging from the glumes they remained lying in the flowering glume and were again enclosed at the time of closing of the flower.

NOTE: All notes were taken from plants growing in a greenhouse.

CLOSING OF FLOWERS.

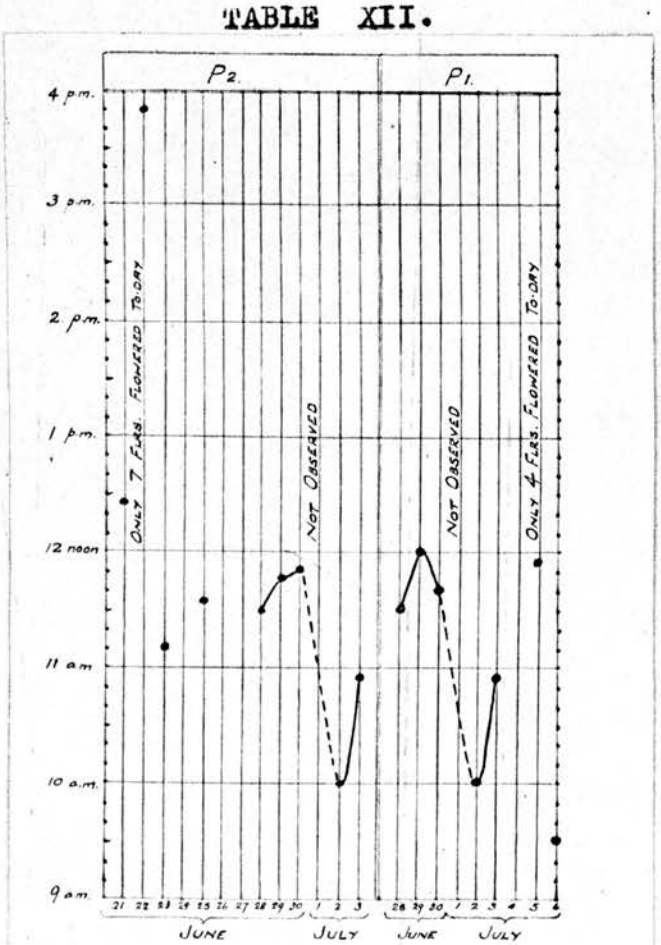
The time which elapsed between the opening and closing of the flowers was very similar to that observed for Italian Ryegrass. The average time taken by hand cross-pollinated flowers was 3 hours.

DAILY FLOWERING PERIOD.

On the great majority of days flowering took place in the forenoon between 9 a.m. and 12 noon, but on/

on some days it was delayed till the late afternoon while on others few or no flowers opened. It is interesting to make a comparison between two morphologically very dissimilar types of perennial Ryegrasses as regards the times at which the first flowers opened. (Table XII). The data unfortunately are very limited, as for the sake of accuracy observations were made when a considerable number of spikes on each plant were mature, and in the second place the one plant had an exceptionally short flowering period. One plant P(1) was of the seeding type, while the other, P(2) produced a large amount of leafage.

TABLE XII.



It is seen that the daily readings for each plant more or less resemble each other.

These results may also be compared with the Italian Ryegrasses. On examining the times for P(1) and those for the Italian Ryegrasses (Table III) it is seen that on the 5th July only 4 flowers of the Perennial, while none in the case of the Italian Ryegrass, opened. On the 2nd July, both Perennials and Italians started to flower at 10 a.m., which was early; and on the 22nd June no flowers of Italian Ryegrass opened while on P(2) which flowered at an unusually late hour, there were only 7.

Even from the small amount of data available it appears that the conditions required for the opening of the flowers to take place are somewhat similar for all three cases. Temperature is not the sole controlling factor as shown before.

TIME TAKEN BY A SPIKE TO COMPLETE FLOWERING.

Under cool greenhouse conditions, a spike of Perennial Ryegrass will usually complete flowering in 10 days, but spikes on some plants took as long as 14 days.

TABLE/

TABLE XIII.

PLANT	No. of FLS. per SPIKELET	Commenced FLOWERING	Finished FLOWERING	No. of DAYS to complete FLOWERING
134	112	13/6	20/6	8
"	109	13/6	20/6	8
"	117	13/6	21/6	9
"	112	13/6	21/6	9
"	114	13/6	21/6	9
	GREENHOUSE CONDITIONS			

A knowledge of the average time a spike takes to complete flowering is useful when it is intended to remove bags after the "infection period" is over. Allowance, however, must be made for the fact that a spike may prolong the flowering period under adverse climatic conditions, and also that the stigmas may remain receptive for several days after the opening of the flowers.

NUMBER OF DAYS TAKEN BY A SPIKE TO RIPEN FROM COMMENCEMENT OF FLOWERING.

Table XIV. gives the number of days taken by spikes of three plants, growing under cool greenhouse conditions, to ripen seed from the day flowering commenced, when the spikes were enclosed in paper bags. The average number of days for 62 plants, when spikes/

spikes were enclosed, was 41.

Spikes enclosed in pollen-proof boxes, outside, ripened more slowly, the average for spikes on 16 plants was 56 days.

TABLE XIV.

PLANT	COMMENCED FLOWERING	RIPE	No.of DAYS.
140(3)	3/6	8/7	35
	4/6	11/7	37
	5/6	8/7	33
142(4)	3/6	15/7	43
	3/6	15/7	43
	6/6	11/7	35
134	4/6	15/7	41
	5/6	21/7	46
	7/6	29/7	52

POLLINATION.

In all cases of controlled pollination the method of isolation employed was:-

(1) In the greenhouse, semi-transparent paper bags and
(2) Outside, pollen-proof boxes.

SELF-POLLINATION.

Autonomous self-pollination was employed throughout the self-pollination experiments, except where/

where otherwise stated, as on examination of the stigmas of enclosed plants the number of pollen grains present equalled that found on stigmas of exposed plants outside which set a normal amount of seed.

During 1923 and 1924 over 50 unrelated plants were selfed at different dates throughout the flowering season. Many of these plants were divided into two pieces; one piece being placed in a greenhouse, the other in the open. In no instance was there any indication that the difference in environment altered self-fertility; neither was there any definite increase as the season advanced. In all plants the degree of self-fertility was low. One plant reached a self-fertility percentage of 12.5%; the majority of plants, however, were below 3%. In 1925 a plant gave a self-fertility percentage of 32.3% (691 flowers - 223 seeds). This is the highest recorded figure so far obtained by me for Perennial Ryegrass. This lack of completely self-fertile plants has made the study of the inheritance of self-fertility in Perennial Ryegrass most difficult.

In 1923 a "wild" plant, No.134, was found on repeated selfing to be 4.2% self-fertile; in 1924 4.8%, and in 1925, when a large piece of this plant was/

was isolated in a greenhouse and left exposed, 4.8% (1558 flowers - 75 seeds). This plant was crossed in 1923 with plant 41, of cultivated origin, which was .6% self-fertile (average of 22 selfings - 2224 flowers, 14 seeds).

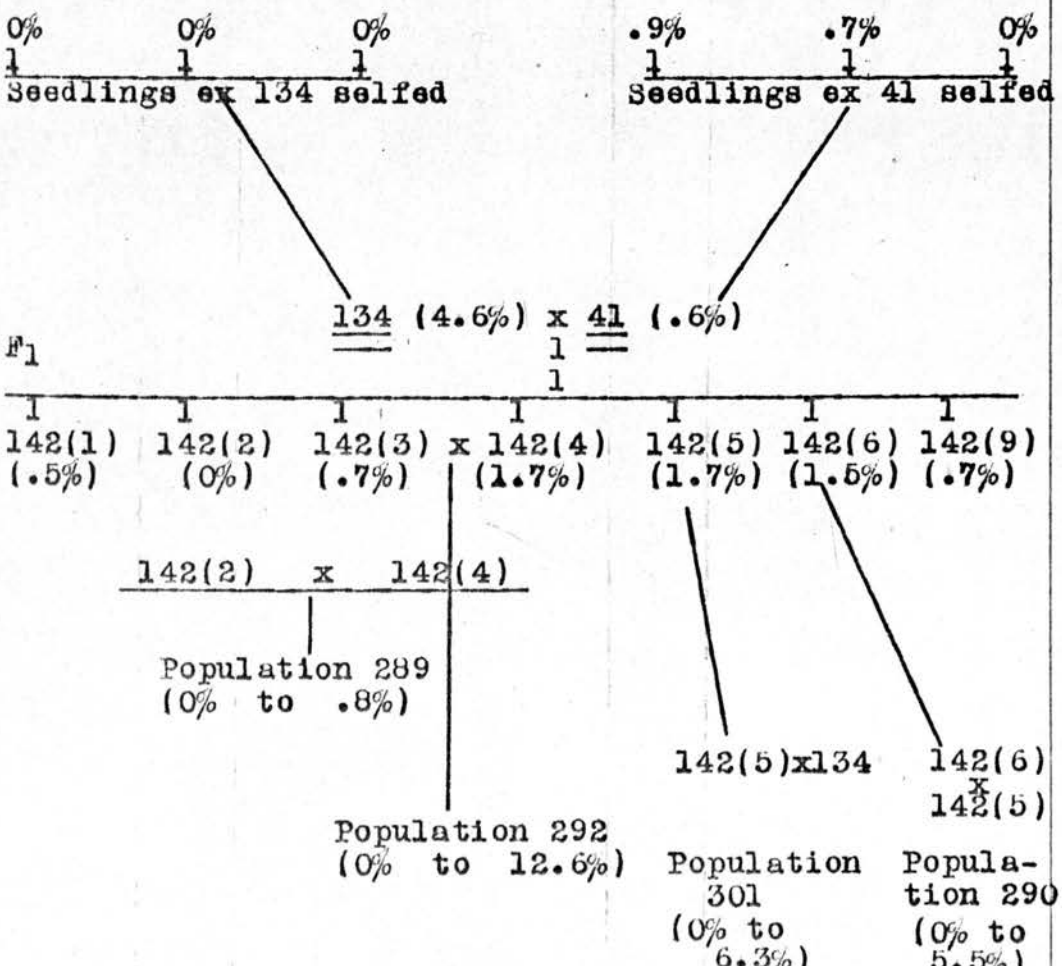
The percentages of flowers producing seed on individual spikes (each spike being considered a unit and separately isolated) showed a slight range, which is only natural, considering the small number of seeds produced per spike. In the case of plant 134, the range was from 3.6% to 6.6%, and for plant 41, from 0% to 1.9%. This range was due, not to "seasonal" fertility, as was shown by the fact that, when several spikes flowered on the same date, the range was still in evidence, but to error of sampling. For the percentages of 22 single spikes of plant 41, the Probable Error was calculated, and was found to be .049 which proves the percentages are reasonably accurate.

It is not possible to calculate the Probable Error for the percentages of every plant, as the number of spikes selfed is often insufficient, owing to practical difficulties. It is in such cases as the present, where the difference in the self-fertility percentages of the plants is so small, that a knowledge/

knowledge of the Probable Error of the individual selfings for each plant is invaluable.

The self-fertility percentages for seven F_1 plants of the cross 134 x 41 were determined in 1924 and 1925, and the range was found to be from 0% to 1.7%. Selfed seedlings were also raised from both 134 and 41. Those from plant 134 yielded no seed when selfed; they showed great want of vigour not noticeable in the seedlings from selfed seed of 41.

In 1924 several of the F_1 plants were intercrossed. The seeds were sown in the autumn and the seedlings came into flower during the summer of 1925. The following diagram shows the experiment in detail.



Tables XV and XVI give the figures obtained on selfing for the individual plants of two of the populations (290 and 292). Table XVI in addition to giving the self-fertility percentages shows the exposed natural seeding percentages.

TABLE XV.

SELFING of INDIVIDUALS in POPULATION 290

PLANT NO.	No.of FLOWERS	No.of SEEDS	DATE of SELFING	PERCENTAGE FLOWERS SETTING SEED
290(20)	128	7	10/6	5.5
(15)	148	6	"	4.1
(21)	84	3	11/6	3.6
(8)	108	3	"	2.8
(12)	126	3	10/6	2.4
(5)	128	3	11/6	2.3
(19)	152	3	9/6	2.0
(13)	171	3	10/6	1.8
(25)	136	2	10/6	1.5
(28)	147	2	9/6	1.4
(3)	112	1	11/6	.9
(14)	126	1	11/6	.8
(30)	144	1	11/6	.7
(18)	140	1	9/6	.7
(32)	135	1	10/6	.7
(22)	157	0	"	0
(11)	146	0	"	0
(31)	144	0	"	0
(17)	168	0	"	0
(16)	134	0	11/6	0
(4)	133	0	15/6	0
(7)	136	0	10/6	0
(9)	126	0	11/6	0
(1)	66	0	15/6	0
(29)	73	0	"	0

TABLE XVI.

SELFING of INDIVIDUALS in POPULATION 292.

PLANT NO.	No.of FLOWERS	No.of SEEDS	DATE of SELFING	PERCENT SELFED FLS. Setting Seed.	PERCENT EXPOSED FLS. Setting Seed.
292(13)	87	11	4/6	12.6	78
(4)	92	8	9/6	8.7	88
(27)	136	8	3/6	5.9	--
(20)	108	5	9/6	4.6	76
(32)	118	4	9/6	3.4	81
(2)	77	1	9/6	1.3	71
(21)	112	1	3/6	.9	--
(33)	147	1	4/6	.8	46
(18)	144	1	4/6	.7	77
(37)	162	1	5/6	.6	75
(19)	269	0	4/6	0	42
(36)	135	0	4/6	0	62
(29)	133	0	9/6	0	48
(10)	84	0	9/6	0	--
(19)	269	0	4/6	0	--

It was found that the self-fertility percentages obtained when enclosing one spike or several spikes together were very similar. Table XVII gives the figures obtained. An increase in the self-fertility percentages, however, resulted when a very large supply of pollen was applied to the stigmas by hand at the time the flowers opened naturally.(Table XVIII) This increase is no doubt due to the increase in the pollen supply, but as yet no satisfactory explanation as to the "cause" is available.

TABLE/

TABLE XVII.

SELFING SINGLE SPIKES and MORE THAN ONE SPIKE

PLANT NO.	SINGLE SPIKES ENCLD.		MORE THAN ONE SPIKE enclosed (together)		SINGLE SPIKES	MORE THAN ONE SPIKE	DATE of ENCLOSING
	No.of FLS.	No.of SEEDS	No.of FLS.	No.of SEEDS	% SELF-FERT.	% SELF-FERTILITY	
301(1)	128	4	253	6	3.1	2.4	9/6
(2)	152	0	375	6	0	1.6	5/6
(3)	176	0	672	1	0	.1	3/6
297(5)	151	1	1134	8	.7	.7	2/6
(8)	168	0	1185	1	0	.8	"
296(4)	158	0	277	0	0	0	9/6
292(20)	108	5	222	10	4.6	4.5	"
(33)	147	1	316	3	.8	.9	4/6
(36)	135	0	296	1	0	.3	"
(37)	162	1	276	7	.6	2.5	5/6
286(1)	120	1	251	3	.8	1.2	3/6
276(1)	156	0	506	1	0	.2	29/6
(2)	90	0	144	0	0	0	3/6
TOTALS	1851	13	5907	47	.7	.8	

TABLE XVIII.

AUTONOMOUS and HAND SELF-POLLINATION

PLANT NO.	AUTONOMOUS SELFING			HAND SELFING			AUT. SELFING	HAND SELFING
	No.of FLS. Selfed	No.of SEEDS	DATE of Enclo-sing	No.of FLS. Selfed	No.of Seeds	DATE of Self-ing	% FLS. Setting Seed	% FLS. Setting Seed.
286(1)	78	10	20/7	17	4	20/7	12.8	23.5
						21/7		
309(0)	-	-	-	8	2	16/7	-	25
298(28)	-	-	-	37	6	31/7	-	16.2
(6)	73	5	5/8	23	3	5/8		
						8/8	6.9	13.
(36)	-	-	-	24	3	20/7	-	12.5
(32)	-	-	-	27	3	6/8		
						8/8	-	11.1
280(2)	77	1	26/6	11	1	16/7	1.3	9.1
298(8)	-	-	-	36	3	21/7		
						30/7	-	8.3
(26)	-	-	-	85	6	30/7	-	7.1
(18)	-	-	-	16	1	25/6	-	6.3
298(33)	-	-	-	36	2	26/6		
						1/7	-	5.6
288(0)	-	-	-	120	6	20/7		
						31/7	-	5.0
276(1)	156	0	29/6	71	3	16/6	0	4.2
279(1)	142	1	9/6	53	1	30/6		
						2/7	.7	1.9
280(1)	63	0	16/7	20	0	20/7		
						21/7	0	0
298(1)	-	-	-	8	0	21/7	-	0

POLLEN TUBE GROWTH.

The following experiments were carried out during the summer of 1925 in order to determine the behaviour of perennial ryegrass pollen when:-

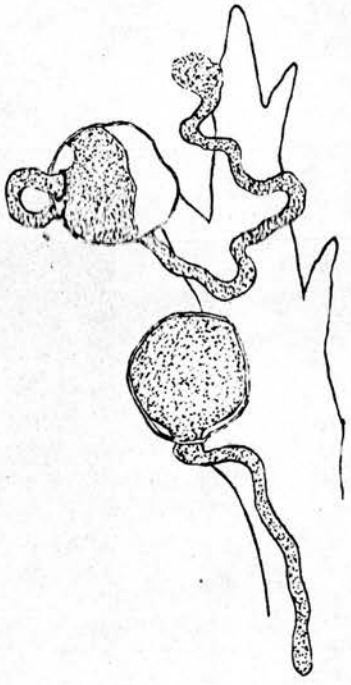
(1) it was applied to stigmas in the plant on which it developed and
(2) to stigmas on other cross-fertile plants.

Various methods of staining and mounting were tried, but unfortunately no satisfactory method was found till late in the season, when the grasses in the greenhouses had practically finished flowering. The few observations made, however, are of some interest.

The following is the method of examination employed. All flowers to be experimented with were emasculated and enclosed in pergamine paper bags. These flowers on opening naturally were either self- or cross-pollinated by hand. The stigmas were afterwards examined at intervals of 20 and 45 hours.

STAINING and MOUNTING.

The pollinated stigmas were carefully separated from the ovaries and mounted direct in a dilute solution of cotton blue in lactic phenol (0.1 gms. cotton blue to 100 cc. lactic phenol. The lactic phenol/



SELF-POLLINATION. GERMINATION
OF POLLEN GRAINS (x 480 approx.)

phenol formula is as follows - lactic acid, phenol, glycerine and water in equal parts. Watkins (1925)). The slides were examined shortly after mounting and the pollen tube development was easily followed.

On examination of stigmas of plant 298 (33) pollinated 20 hours previously, it was found that pollen grains on both self and cross-pollinated stigmas had germinated, but in the case of the self-pollinated stigmas several of the pollen tubes were growing on the surface of the stigma branches, a few were growing away from the central column and the remainder were growing down the branches of the stigma normally. A few cases of surface growth were also observed on the cross-pollinated stigmas. 45 hours after pollination, tubes of the self-pollinated stigmas had grown little or no further than those examined after 20 hours, while many tubes on the crossed stigmas had entered the thick central column. The number of empty pollen grains was now much greater on the cross pollinated than on the self-pollinated stigmas. (Plant 298(33) was known to have a low self-fertility percentage, - 5.5% hand selfing - functional pollen and female organs.)

From the above experiment it will be seen that/

that pollen from a plant of low self-fertility when applied to stigmas on the same plant did germinate, and that the rate of growth of the pollen tube down the stigma was not constant as observed by EAST (1918) and ANDERSON (1924) in Nicotiana, and by KNIGHT (1917) in Apples, but growth appeared to be retarded after the pollen tube had travelled a short distance in the stigma branches. It was noticed, however, that a few pollen tubes had reached a considerable length 45 hours after pollination, but none were observed to enter the central column. This case may resemble the growth of pollen tubes in the styles of incompatible varieties of plums (CRANE 1925) where incompatibility was found to be due to inhibition occurring shortly after penetration of the pollen tubes. Another instance of inhibited pollen tube growth is given by KARPECHENKO (1924). He obtained seed from Raphanus sativus L. x Brassica oleracea L., but the reciprocal cross gave no results. He also failed to get seed from B. cleracea x R. raphinistrum L. and R. odessoinus Spreg. The cause of this sterility was found to be due to Raphanus pollen on stigmas and in pistils of cabbages producing only short tubes, or not germinating at all. JOST 1907 (East, Study I p.518) noted self sterility in Secale cereale (var. montanum).

When/

When flowers were crossed, the pollen tubes were found to have penetrated the micropyle in about 8 hours after pollination; after self pollination, the tubes had merely reached the base of the pistil after 24 hours.

CORRENS 1912 (East, Study I p.519) working with Cardamine pratensis, a self sterile species, found that pollen grains germinated on the stigmas of the self-pollinated flowers, but produced only short tubes that did not penetrate the tissues of the stigmas. While after cross-pollination the pollen tubes were found in the upper part of the ovaries after only 48 hours.

The following is a quotation from WESTGATE (1915), who worked with Trifoleum pratense.

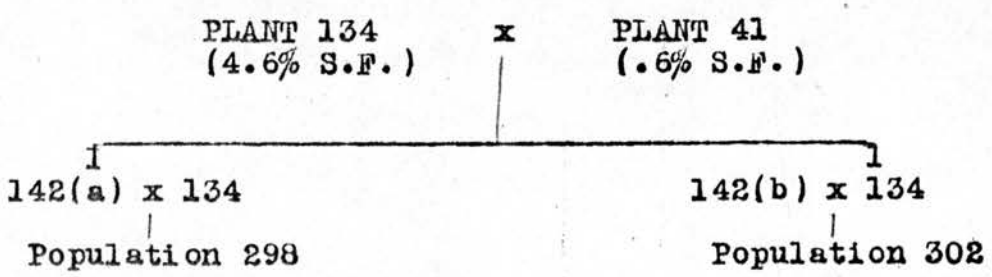
"An examination of 30 flowers which had been self-pollinated for 55 hours showed good germination on the stigmas, but no fertilisation. The pollen tubes made a slow growth and none exceeded 4 mm. in length. In flowers which had been self-pollinated for 90 hours, one pollen tube attained a length of 7.5 mm., while the rest were 5 mm. or less in length. The pistils of red clover average 12 mm. in length. Eggs were found to be disintegrating four days after the/

the flowers opened. An examination of 30 flowers which had been cross-pollinated for 55 hours showed that fertilisation had taken place in all of them".

BEAUMONT and WILCOX (1922) indicate that in prunus both self sterility and cross-sterility may be accounted for by the lack of proper stimulation both for germination of the pollen on the stigma and for the growth of the tube in the style.

CROSS STERILITY.

When investigations into methods of breeding were being carried out during 1924, it was found that certain plants, when crossed, produced few seeds. It was, therefore, decided to carry out crossing experiments in 1925. In the experiments two inbred populations were selected. Their pedigree is as follows:-



Plants of both population 298 and 302 were crossed back to the parent 134 (134 being used as the male).

METHOD.

Plant 134 was multiplied vegetatively in pots/

pots during the autumn of 1924 in order to insure a sufficient supply of pollen throughout the course of the experiment. The seeds obtained from the crosses 142(a) x 134 and 142(b) x 134 were sown in sterilised soil(heated soil free from foreign seeds) in September 1924. The seedlings were transplanted in 5½" pots in which they remained throughout the whole experiment. The two populations, together with plant 134 were isolated in a cool greenhouse.

When the spikes appeared, on the plants of the populations 298 and 302, only two per plant were permitted to develop. All flowers on these spikes except 2 per spikelet were removed and these were emasculated. The spikes were isolated in pergamine bags. Owing to the transparent nature of these bags, their removal was not necessary except at the time of pollination.

POLLINATION;

Only flowers which had newly opened were pollinated with pollen from freshly dehiscing anthers of plant 134. This method was followed during the whole experiment as it had been previously ascertained that both the pollen and stigmas are functional at that stage of development.

THE/

THE METHOD OF RECORDING THE CROSS FLOWERS was as follows:-

Diagrams of the spikes on each plant were drawn and were numbered (1) and (2); the spikelets on each spike were numbered 1. 2, 3, and so on, from the apex of the spike downwards. The basal flower of each spike was denoted by (1), the second flower by (2). In this way records of each pollination were easily noted. When the seeds had developed the numbers of the flowers setting seed, as well as those which failed to produce seed, were noted.

The results of the crosses are given in Tables XIX and XX.

TABLE XIX.

POPULATION 302.

PLANT NO.	No.of SPIKE	No.of FLS. Crossed	No.of SEEDS	TOTALS No.of FLS. Crossed	TOTALS No.of SEEDS	DATES	%
302(0	1	2	2				
"	2	4	4	6	6	12/6	100
302(3	1	4	4	4	4	13/6-15/6	100
302(18	1	36	35				
"	2	17	17	53	52	11/6-13/6	98
302(17	1	17	17				
"	2	10	9	27	26	11/6-13/6	96
302(8	1	11	10				
"	2	13	13	24	23	17/6-18/6	96
302(9	1	18	17				
"	2	11	10	29	27	13/6-17/6	93
302(4	1	16	15				
"	2	10	9	26	24	13/6-19/6	92
302(19	1	27	24				
"	2	6	6	33	30	12/6-13/6	91
302(11	1	16	12				
"	2	10	10	26	22	12/6-13/6	85

TABLE XIX (cont.)

PLANT NO.	No.of SPIKE	No.of FLS. Crossed	No.of SEEDS	TOTALS No.of FLS. Crossed	TOTALS No.of SEEDS	DATES	%
302(13)	1	20	14				
"	2	15	13	35	27	11/6-13/6	77
302(6)	1	5	4				
"	2	9	6	14	10	15/6-19/6	71
302(15)	1	14	9	14	9	12/6-17/6	64
302(10)	1	16	9				
"	2	11	6	27	15	11/6-13/6	56
302(5)	1	16	9				
"	2	9	5	25	14	11/6-13/6	56
302(2)	1	8	2				
"	2	12	1	20	3	13/6-15/6	15
302(16)	1	10	0				
"	2	7	0	17	0	19/6 -	0

TABLE/

TABLE XX.

POPULATION 298

No.of PLANT	No.of FLS. Crossed	No.of SEEDS	DATES	% AGE
298(36)	19	19	13/6 - 15/6	100
" (32)	6	6	15/6 -	100
" (38)	6	6	15/6 - 16/6	100
" (18)	5	5	13/6 - 15/6	100
" (23)	5	5	15/6 -	100
" (33)	4	4	15/6 - 16/6	100
" (35)	3	3	22/6 -	100
" (4)	2	2	19/6 -	100
" (24)	2	2	15/6 -	100
" (20)	2	2	16/6 -	100
" (11)	1	1	19/6 -	100
" (21)	1	1	15/6 -	100
" (8)	17	16	15/6 - 17/6	94
" (30)	13	12	15/6 - 16/6	92
" (7)	23	21	15/6 - 18/6	91
" (5)	8	7	17/6 -	88
" (31)	7	6	17/6 - 19/6	86
" (28)	12	10	15/6 -	83
" (15)	17	14	17/6 - 19/6	82
" (19)	14	11	15/6 - 18/6	79
" (6)	13	10	13/6 - 15/6	77
" (10)	13	10	15/6 - 17/6	77
" (26)	18	13	16/6 - 19/6	72
" (16)	17	12	12/6 - 15/6	71
" (2)	20	14	17/6 - 22/6	70
" (17)	10	7	15/6 -	70
" (9)	10	7	13/6 - 17/6	70
" (37)	11	6	17/6 - 22/6	55
" (12)	6	3	17/6 -	50
" (0)	4	2	18/6 - 19/6	50
" (27)	9	2	17/6 - 19/6	22
" (39)	15	3	16/6 - 19/6	20
" (13)	14	2	15/6 - 16/6	14
" (25)	17	0	15/6 - 17/6	0
" "	18	0	25/7 -	0

As will be seen from the tables the two plants 302(16) and 298(25) failed to produce seed when crossed back to plant 134. Further, these two plants also failed to produce seed when intercrossed (302(16) x 298(25) - (10 flowers crossed gave no seed). The female organs of both 302(16) and 298(25) were proved to be functional as follows:-

302(16) x plant 286 - 9 flowers set 8 seeds

298(25) x plant 277 - 6 flowers set 6 seeds

There was no doubt that the pollen of 134 was functional, as seeds were readily obtained by its application to the stigmas of other plants in the populations.

Two plants 298(18) and 298(33) in the population 298 were found to be cross-sterile. Both these plants were cross-fertile with 134 proving that their female organs were functional; and when pollen from 298(33) was applied to plant 277, seeds were set, showing that the pollen of 298(33) was also functional.

298(18) x 298(33) - 33 flowers set 1 seed

277 x 298(33) - 7 flowers set 6 seeds

OBSERVATIONS ON SEED PRODUCTION WITHIN CLONES

CLONE 41. In 1923 plant 41 was divided into 200 pieces. Three beds of 64 pieces were planted, the pieces being 9" apart each way. Plants in bed 1 were allowed/

allowed to flower normally; plants in bed 2 were cut back early and came into full flower after bed 1, while those in bed 3 were cut back twice and came into flower late in the season.

Counts of the percentages of flowers setting seed were made during the summer. The results are given in Table XXI.

TABLE XXI.

NATURAL POLLINATION. CLONE 41.

DATE of COUNTING	APPROX. DATE of FLOWERING	No.of FLOWERS	No.of SEEDS	% FLS. SETTING SEED
10 July	10 June	147	18	12.
		165	15	9.1
		154	12	7.8
		144	10	6.9
		128	0	0
26 July	26 June	127	61	48.
		117	44	38.
		134	46	34
		132	43	33
		127	42	33
		120	40	33
		131	42	32
		89	23	26
		135	33	24
		112	25	22
15 Aug.	15 July	136	19	14
		104	15	14
		104	9	8.7
		102	4	3.9
		128	4	3.1
		112	3	2.7
18 Sept.	15 Aug.	105	7	6.7
		98	5	5.1
		119	6	5.0
		120	5	4.2
		104	4	3.8
		112	4	3.6

TABLE XXI. (cont.)

DATE of COUNTING	APPROX. DATE of FLOWERING	No. of FLOWERS	No. of SEEDS	% FLS. SETTING SEED
18 Sept.	15 Aug.	90	3	3.3
		124	4	3.2
		105	3	2.9
		104	3	2.9
		128	3	2.3
		91	2	2.3
		86	2	2.3
		83	1	1.2
		94	1	1.1
		98	1	1.0
		96	1	1.0
		126	0	0
		91	0	0
6 Oct.	After 15 Aug.	110	16	15
		85	11	13
		78	9	12
		118	12	10
		114	9	7.
		105	8	7.5
		42	3	7.1
		112	6	5.4
		72	3	4.2
		126	3	2.4

It is seen that the percentages were low in the early part of the season (10 June) increasing to a maximum about 26th July. After that the percentages fell until the 15th August. After this date a slight increase is again noticed. This increase is probably due to

(1) more wind to increase the dispersal of pollen and (2) the flowering of 2nd crop hay in the neighbourhood.

During/

During the summer spikes of this clone were isolated in pollen proof boxes. The results are given in Table XXII. The figures resemble closely those obtained under greenhouse conditions. Where 2 spikes from different pieces were enclosed together, the percentages were not increased.

TABLE XXII.

SELF-POLLINATION. CLONE 41.

No. of FLOWERS	No.of SEEDS	% FLS. SETTING SEED	NOTES
98	0	0	) Single spikes enclosed in
96	1	1	) separate boxes.
104	0	0	)
84	1	1.2	) Two spikes from one piece
64	0	0	) selfed together.
105	2	1.9	) Four spikes from one piece
66	1	1.5	) selfed together.
103	1	1.0	)
110	0	0	)
96	1	1.0	) Two spikes from different
105	1	1.0	) pieces enclosed together
126	1	.8	) Two spikes from different
112	0	0	) pieces enclosed together.
88	1	1.1	) Two spikes from different
94	1	1.1	) pieces enclosed together.
119	0	0	) Two spikes from different
100	0	0	) pieces enclosed together.
98	1	1.0	) Two spikes from different
102	0	0	) pieces enclosed together.
112	1	.9	) Two spikes from different
136	1	.7	) pieces enclosed together.
Average % age		.7	

CLONE 134.

64 pieces of plant 134 were planted in a bed in a field, near several hundred plants of perennial ryegrass grown for selection. Readings were taken of the percentages of flowers setting seed. The surrounding plants were kept cut during July, but were flowering in August. This accounts for the increase during that month.

TABLE XXIII.

NATURAL POLLINATION - CLONE 134

APPROX. DATE of FLOWERING	No. of FLOWERS	No. of SEEDS	% FLS. SETTING SEED
20 July	156	35	22
	104	8	7.7
	86	6	7.0
	121	8	6.6
	91	6	6.6
After 1st. Aug.	158	52	33
	117	37	32
	114	31	27
	68	18	27
	126	23	18
	98	15	15
	128	19	15
	168	18	11
	144	11	7.6
	165	11	6.7
	112	3	2.7

NATURAL/

NATURAL SEEDING.

F_1 plants of the cross 134 x 41 were planted in a bed and allowed to seed naturally. Percentages of flowers setting seed on spikes which flowered about 14th June were calculated. As will be seen from the table the percentages for different plants flowering about the same date resemble each other closely. This is also true for spikes on a single plant. It was noticed that the percentages of the first plant to flower in the bed were low.

TABLE XXIV/

TABLE XXIV.

NATURAL POLLINATION - F_1 PLANTS of the CROSS 134 x 41

PLANT	No.of TILLERS on 22/2/24	APPROX. DATE of FLOWERING	No.of FLS.	No.of SEEDS	% FLS. SETTING SEED
139(3)	9	1/6	178	38	21
			154	28	18
			148	23	16
			132	28	21
142(2)	14	14/6?	104	81	78
			64	46	72
			84	57	68
142(3)	9	14/6	101	70	69
			81	41	51
			96	55	57
142(4)	17	14/6?	68	51	75
			67	49	73
142(5)	25	14/6	118	78	66
			143	93	65
			100	63	63
			150	93	62
			138	79	57
142(6)	23	14/6	114	68	60
			144	86	60
			112	67	60
			136	81	59
			123	71	58
			173	98	57
142(7)	17	14/6	111	67	60
			153	91	59
			128	72	56
			114	55	48
142(10)	25	14/6	153	120	78
			170	129	76
			144	102	71
			167	114	68
			155	99	64

All these plants were sown in the autumn of 1923. In February 1924 their tillers were counted, in order to attain a rough indication of the vigour, mainly from the leaf production point of view, of the seedlings. These figures are entered in the second column of the table. It is seen that no reduction in fertility, under the above conditions, is noticeable for these leafy plants when compared with plants having a lower number of tillers.

CROSS-POLLINATION BY HAND.

Many experiments were carried out with a view to determine the correct time for pollen to be applied to the stigma. The most certain results were obtained when fresh pollen was applied at the time of opening of the flowers, but good settings resulted when flowers were pollinated 24 hours after opening.

The percentages of flowers setting seed when pollinated at the time of opening were extremely high. In one case 30 flowers gave 30 seeds, and in another 53 flowers set 52 seeds. These high percentages are no doubt due to the fact that in the case of hand pollination all but the best developed flowers on a spike are removed and these remaining flowers receive an ample supply of pollen.

Results/

Results were disappointing when fresh pollen was applied to the stigmas in the evening. In such instances the percentages were very considerably reduced.

THE APPLICATION OF "STALE" POLLEN TO THE STIGMA.

The pollen of perennial ryegrass experimented with only remained viable for a very limited period. Pollen was collected at the time of dehiscence and kept in a dark place in cotton-wool plugged specimen tubes for 24 hours before being applied to the stigmas of cross-fertile plants.

The results obtained were variable. In one plant 33% of the flowers so pollinated produced seed, but in other cases fertilisation did not take place. From the figures obtained it is probable that the period for which pollen remains viable varies according to the plant on which it develops.

The fact that pollen loses its viability so rapidly is unfortunate, as considerable trouble is experienced in arranging for two intended parents to flower simultaneously.

TALL OAT GRASS.

ORDER OF FLOWERING.

The branches of the panicle are closely apposed to the main axis until within a short time of flowering and return again more or less to their original position when flowering is finished.

Usually a spikelet contains two flowers, the lower being staminate, the upper hermaphrodite.

The flowering of the panicle proceeds regularly from the apex downwards. In the spikelet, the staminate, or lower flower, usually opened before the hermaphrodite one, but the interval between the opening of the two is not great.

OPENING OF FLOWERS.

Before the commencement of opening the two flowers of a spikelet, which have been lying in close contact with each other up till now, separate. The period between the opening of the flowers and dehiscence of the first anthers was generally less than 5 minutes (greenhouse conditions).

Examples:-

9.55 a.m.	Staminate flower opening.
10. a.m.	First anther dehiscing.
10.18 a.m.	Remaining two anthers dehiscing.
9.57 a.m.	Pistilate flower opening.
10.½ a.m.	First anther dehiscing.

The/

The daily flowering period under greenhouse conditions was from 8 a.m. to 9.30 a.m. This period varies according to weather conditions.

CLOSING OF FLOWERS.

The closing of the flower may occur within an hour from the time of opening, but as a rule flowers take 1-2 hours or more to close. Shortly after the flower has closed, or while it is yet slightly open, the two flowers of the spikelet begin to come together, assuming their original position within 3-4 hours.

In about 10 days from the time the first flowers open, the branches of the upper panicle again approach the main axis. The remainder follow in a few days. Fourteen days (approx.) is the time taken for the whole panicle to flower under greenhouse conditions.

TIME TAKEN BY A PANICLE TO RIPEN SEED FROM THE COMMENCEMENT OF FLOWERING.

The interval under greenhouse conditions is approximately 33 days, and several days longer when the plant is grown outside.

SELF-POLLINATION/

SELF-POLLINATION.

Both plants of commercial and "wild" origin were selfed at intervals throughout the flowering season.

A high degree of self-sterility was evident in all 20 plants worked with. As the flowering season advanced, no definite alteration in the percentages of flowers setting selfed seed was found. Several plants were divided into three, and each piece was kept under a different condition, and in no case was any significant difference in the percentages observed.

Self-fertility ranged from 0% to 6.8%.

Some of the results are found in Table XXV.

TABLE XXV.

SELF-POLLINATION.

PLANT	DATE of ENCLOSING	CON-DITIONS	No.of HERMA-PHRODITE FLS.	No.of SEEDS	% FLS. SETTING SEED
TO(1)	5/6	S.H.	95	2	2.1
"	14/6	S.H.	101	4	3.9
"	3/7	S.H.	113	1	.9
"	5/6	L.H.	96	1	1.0
"	14/6	"	106	1	.9
"	16/6	"	64	0	0.0
"	25/6	0	96	1	1.0
"	30/6	"	47	0	0.0
"	22/7	"	132	2	1.5
"	22/7	"	87	1	1.2

Commercial (Fibrous Roots)

TABLE XXV. (cont.)

PLANT	DATE of ENCLOSING	CON-DITIONS	No.of HERMA-PHRODITE FLS.	No.of SEEDS	% FLS. SETTING SEED
TO(2)	5/6	S.H.	128	2	1.6
"	7/6	"	131	0	0.0
"	18/6	"	112	0.	0.0
"	25/6	"	123	0	0.0
"	14/6	L.H.	119	1	0.8
"	14/6	"	131	3	2.3
"	3/7	"	32	0	0.0
"	22/7	"	44	1	2.3
"	17/6	0^x	133	1	0.8
	Commercial (Fibrous Roots)				
TO(A)	30/6	0	153	9	5.9
"	3/7	0	123	7	5.7
"	25/7	"	103	7	6.8
"	25/7	"	92	5	5.4
	Commercial (Fibrous Roots)				
TO(3)	14/6	S.H.	99	0	0.0
"	28/6	"	136	0	0.0
"	3/7	"	103	0	0.0
	"Wild" (weak bulbed)				
TO(B)	18/6	0	128	1	0.8
"	30/6	"	119	0	0.0
"	22/7	"	121	0	0.0
"	22/7	"	143	1	0.7
	"Wild" (bulbous)				

NOTE:

S.H. denotes Small House, heated during winter.
L.H. " Large Cool House
0. " Outside
0^x " Wintered outside, but selfed in L.H.

No definite increase in self-fertility was found when two panicles from one plant were enclosed together.

TABLE XXVI.

SINGLE PANICLES ENCLOSED.

PLANT	No. of HER. FLS.	No.of SEEDS	% FLS. Setting Seed
TO(2)	692	5	0.7
TO(A)	276	16	5.8
TO(B)	249	1	0.4
TO(D)	178	0	0.0

TWO PANICLES FROM ONE PLANT ENCLOSED TOGETHER

PLANT	PANICLE	No. of Her. FLOWERS	No.of SEEDS	% FLS. Setting SEED	AVERAGE %
TO(2)	1	54	1	1.9	1.0
	2	72	0	0.0	
TO(A)	1	103	7	6.8	6.2
	2	92	5	5.4	
TO(B)	1	121	0	0.0	0.4
	2	143	1	0.7	
TO(D)	1	82	0	0.0	0.0
	2	98	0	0.0	

SELFING/

SELFING OF EXPOSED PANICLES.

Panicles on certain plants were isolated by their times of flowering. These plants were allowed to flower exposed. A panicle of TO(1) in the greenhouse flowered exceptionally early before any other tall oat grasses. Another panicle on the same plant flowered some time later, but after the upper half had flowered, another plant TO(2) in the house began flowering. In the first case 116 flowers produced 1 seed, and in the latter 18 seeds were obtained from 41 flowers (= 44%) on the upper portion of the panicle, while on the lower, 100 flowers gave 72 seeds.

A panicle on another piece of plant TO(1) growing in the large house was left exposed (18th July) when another exposed plant, which was comparatively isolated from it, was flowering, gave 4 seeds from 39 flowers = 10% (103 seeds were obtained from 124 flowers = 83%, when a panicle of TO(1) was exposed in the presence of other plants in full flower). The following table gives a few more examples where plants proved to be self-sterile or almost so on isolation by time of flowering.

TABLE/

TABLE XXVII.

EXPOSED SELFING.

PLANT	DATE of FLOWERING	CONDI-TIONS	No. of HERMA-PHRODITE FLS.	No. of SEEDS	% FLOWERS Setting SEED
TO(V)	11/7	S.H.	118	1	0.8
TO(XV)	29/7	0	303	18	5.9
		0	273	16	5.9
		0	142	8	5.6
TO(XVI)	17/8	0	97	0	0.0
		0	105	0	0.0
		0	124	0	0.0

S.H. = Small House.
0 = Outside.

T.O.(1) x T.O.(1)

For this experiment 2 pieces of tall oat grass T.O.(1) - which was divided in the autumn of 1923 - were subjected to different climatic conditions; one being kept in a small house which was heated during the winter; and the other potted and placed outside. In the spring the latter piece was brought into a large cool house shortly before flowering. It was hoped that as a result of this treatment certain changes in the constitution of the two pieces would/

would occur which would permit of the production of seed when they were intercrossed. This expectation was not realised, however, for the percentage of flowers setting seed did not exceed the percentage obtained when each piece was selfed separately.

NOTE: The female parent was emasculated and pollen from the male parent applied by hand.

BEHAVIOUR of:-

(1) HERMAPHRODITE

(2) STAMINATE FLOWERS, after POLLINATION.

Unfertilised flowers behave irregularly after pollination, either remaining open for a considerable period, or closing only to re-open later.

Non-fertilisation of the hermaphrodite flower in a spikelet does not in any way influence the behaviour of the staminate flower.

After pollination resulting in fertilisation, the flowers close and do not open again.

TABLE XXVIII.

TABLE XXVIII.

TO(1) × TO(1)

HERMAPHRODITE FLOWERS (POLLINATED UNFERTILISED)										STAMINATE FLOWERS.								
Flower No.	Date 16/6 Time 12	Date 17/6 Time 9.40		Date 17/6 Time 4.20	Date 18/6 Time 6 p.m.	Date 19/6 Time 5.45	Date 20/6 Time 11.15	Date 21/6 Time	Date 23/6 Time 11	Flower No.	Date 16/6 Time	Date 17/6 Time 9.40	Date 17/6 Time 4.20	Date 18/6 Time 6-	Date 19/6 Time 5.45	Date 20/6 Time 11.15	Date 21/6 Time	Date 23/6 Time 11.
1		50	POLLINATED 17/6 9.40 a.m.	C	C	C	50	50	50	1	-	-	-	-	-	-	-	-
2		50		C	C	C	50	50	50	2		50	C	C	C	C	C	C
5		50		0	0	½0	50	50	C	5				0.	C	C	C	C
9		0		C	C	C	50	C	C	9		0	C	C	C	C	C	C
12		0		C	C	C	C	50	50	12		0	0	0	0	0	C	C
14		0		C	C	C	C	C	C	14		0	C	C	C	C	C	C
16		0		C	C	50	50	50	C	16		0	C	C	C	C	C	C
18		0		½0	0	0	0	½0	½0	18		0	C	C	C	C	C	C

TO(1) × TO(2)

HERMAPHRODITE FLOWERS POLLINATED - FERTILISED.								
Flower No.	Date 19/6 Time 9.10		Date 19/6 Time 5.40	Date 20/6 Time 11.10	Date 21/6 Time	Date 23/6 Time 11.30	Date 24/6 Time 4 p.m.
1	OG	POLLINATED 19/6 9.10 a.m.	C	C	C	C	C
2	OG		C	C	C	C	C
3	0		C	C	C	C	C
4	0		C	C	C	C	C
5	0		C	C	C	C	C
6	0		C	C	C	C	C
7	0		C	C	C	C	C
8	0		C	C	C	C	C

OG denotes Opening
0 " Open
½0 " ½ open
50 " slightly open
C " closed.

PERIOD DURING WHICH THE STIGMAS REMAIN RECEPTIVE.

Crosses were made between plant T.O.(1) and T.O.(2). Firstly, pollen from T.O.(2) was applied by hand to emasculated flowers of T.O.(1) which had flowered 24, 48 and 72 hours previously. In all cases a high percentage of flowers set seed. The reciprocal cross gave similar results. The fact that stigmas remain receptive for at least 72 hours after the flower has opened is important from the point of view of seed production under natural conditions.

It was found also that stigmas of T.O.(2) were receptive 72 hours before the flowers opened. For these experiments flowers were opened by fine pointed forceps, emasculated and the stigmas pollinated with "fresh" pollen ex T.O.(1). As each flower so treated opened, the date and time of opening were noted. When immature pollen was used, fertilisation did not follow.

PERIOD DURING WHICH POLLEN REMAINED VIABLE.

Emasculated flowers cross-pollinated by hand with "fresh" pollen set seed abundantly, in several cases 100%. On the other hand flowers of T.O.(2) cross-pollinated with "stale" pollen (24 hours dehisced) ex T.O.(1)) at the time of opening or shortly after/

after gave good results - 71% of the flowers so treated setting seed, as against an average of 96% when freshly dehisced pollen was used. But when "stale" pollen (24 hours dehisced) from T.O.(2) was applied to the stigmas of T.O.(1), no seeds developed, while 97% of flowers pollinated with freshly dehisced pollen from T.O.(2) set seed.

It is seen from the above that the period for which pollen remained viable varied according to the plant on which it was developed.

AVENA PUBESCENS.

A few observations on Avena pubescens may be given here although this grass is of no agricultural importance, since some of the results differ, in certain respects, from any other grass worked with.

ORDER OF FLOWERING.

The order of flowering of the panicle is quite in accordance with other grasses, i.e. regularly from the apex to the panicle downwards; apex of branches of panicle downwards; base of spikelets upwards.

DAILY/

DAILY FLOWERING PERIOD.

The maximum daily flowering period was between 5 and 6 p.m. Only on rare occasions did flowers open before 5 p.m.

TIME TAKEN FROM OPENING OF FLOWERS TILL DEHISCENCE OF ANTHERS.

This varied according to the weather conditions besides slight differences between plants flowering at the same time. The average time was 9 minutes.

TIME TAKEN FOR A PANICLE TO COMPLETE FLOWERING.

The average time for a panicle to finish flowering in the greenhouse was 8 days. At the time the lower flowers open the upper branches return to their original position against the main axis.

SELF-POLLINATION.

Plants for the following experiments were collected from an isolated clump growing locally. These were placed in:

(1) a small house heated during the winter
(2) a cool house and
(3) in the open.

Twenty panicles under the three conditions were enclosed in bags or boxes before flowering.

Result:- 3301 flowers set no seed.

NATURAL/

NATURAL SEEDING.

It was found that flowers freely exposed, under the conditions stated above, gave no seed. This result may be due to the transplanting, but this is very unlikely, as on examination of the original clump (growing wild) the same sterility was evident. The most probable explanation at present is, that the wild clump originated from a single plant by vegetative multiplication and is self-sterile. The sterility was certainly not due to want of pollen.

CONTROLLED CROSS-POLLINATION.

Several hundred flowers were kept under strict observation, and many crosses were made. Stigmas were pollinated from 72 hours before the opening of the flowers to 72 hours after, with freshly dehisced pollen. In only one flower was a seed developed. The pollen used in this case was 24 hours old, and the flower had been open for 46½ hours.

The behaviour of the flowers after pollination indicated sterility as they remained open.

DAHLGREN (1922) has shown that in Lysimachea Nummularia seeds are set but rarely. He has demonstrated that the reproductive organs of this species are functional in compatible combinations. He, therefore/

therefore, comes to the conclusion that the lack of seed production in populations of L. Nummularia is due to self-sterility, and to the fact that all plants at a place generally are members of the same clone.

Unfortunately, in the case of A. pubescens, material from another district was not available; therefore, all the crosses made were between plants of the same local population.

GOLDEN OAT GRASS.

TIME OF FLOWERING.

All plants observed flowered early each day. The main flowering being completed by 9 a.m., only occasional flowers opening after that time.

TIME TAKEN FROM OPENING OF FLOWERS TILL DEHISCENCE OF ANTHERS.

When flowers on the same plant open within a short time of each other the interval between opening and dehiscence is almost similar.

Times range from 10 to 36 minutes (greenhouse conditions). An example may be given:-

PLANT/

PLANT X.

21 June	9.24 9.58	Flower opening Two anthers dehiscing	= 34 mins.
21 June	9.23 9.57	Flower opening First anther dehiscing	= 34 mins.
24 June	9.18 9.37	Flower opening Anthers dehiscing	= 19 mins.

Under greenhouse conditions panicles take from 6-9 days to flower and approximately 30 days more to ripen.

SELF-POLLINATION.

The 12 plants worked with were raised from a commercial sample of seed. Four of these were divided, one half of each plant was placed outside and the other in the greenhouse.

In only 4 plants was a seed obtained on self-pollination.

The results from the divided plants are given in Table XXIX.

TABLE/

TABLE XXIX.

PLANT	DATE of Enclosing	CONDI-TIONS	No.of SPIKE-LETS	No.of FLS.	No.of SEEDS.	% FLS. Setting SEED.
I	9/6	L.H.	335	1005	1	0.1
	17/6	L.H.	212	636	1	0.16
	19/6	O.	228	684	0	0.0
II	9/6	L.H.	201	603	0	0.0
	14/6	L.H.	79	237	0	0.0
	5/7	O.	156	468	0	0.0
	27/7	L.H.	147	441	0	0.0
III	17/6	L.H.	251	753	0	0.0
IV	17/6	L.H.	342	1026	0	0.0
	4/7	O.	461	1383	0	0.0

L.H. = Large Cool House.
O. = Outside.

N.B. The flowers on these panicles were not directly counted. The spikelets were counted accurately and these figures were multiplied by 3 (average number of flowers per spikelet).

Three normal panicles on plant II were allowed to flower exposed in the greenhouse. (27 July). At this time there was a panicle on another plant flowering in the same house, but fairly well isolated from plant II. When the panicles of plant II were examined, it was found that only 4 flowers had set seed. The figures are as follows:-

1491 flowers 4 seeds = .3%.

TIMOTHY.

Flowering generally takes place before 9 a.m., a very few flowers opening after that.

Under greenhouse conditions the flowering of an average panicle is completed in a week.

SELF-POLLINATION.

The different plants of Timothy under observation showed great variation in the degree of self-fertility. A few plants proved to be almost completely self-sterile, e.g. 3 panicles of Cb 36 were selfed and from 2715 flowers on these panicles only 7 seeds were obtained (= .25%) while on the other hand 767 flowers produced 615 seeds on plant Cb 26 (= 80%).

Difficulty was experienced in counting the number of flowers per panicle. When dealing with naturally pollinated panicles where the number of unfertilised flowers was small, the simplest method was found to be the determination of the number of seeds plus the number of unfertilised flowers. But generally on self-fertilised panicles the number of unfertilised flowers was high, and owing to the great chance of error in counting large numbers of such flowers, the following method was employed for all self/

self-pollinated panicles.

It was found that, by counting the number of flower stalks on the main axis - under a dissecting microscope - after the removal of the flowers, a reasonably accurate determination of the total number of flowers per panicle was possible. The figures thus obtained are too low, as the number of flowers on naturally pollinated panicles counted in this manner were exceeded by the figures obtained, when the number of unfertilised flowers were added to the number of seeds, e.g.

PANICLE (1).

Total No. of flowers on panicle (Stalk method) 1496
" " " " " " (Unfer. Fls. plus seeds) 1605

PANICLE (2).

Total No. of flowers on panicle (Stalk method) 1457
" " " " " " (Unfer. Fls. plus seeds) 1566

The difference is due to some of the smallest stalks being overlooked in counting. It is, therefore, seen that the percentages of fertile flowers on self-pollinated panicles are slightly too high. In the case of naturally pollinated panicles, the number of unfertilised flowers was small and were counted easily, thus the figures in the table are more or/

or less accurate.

In the following table are given the results of self-pollination.

TABLE XXX.

SELF-POLLINATION

PLANT	No.of FLOWERS	No.of SEEDS	% FLOWERS Setting SEED	NOTES
36	2715	7	0.25	
32	895	20	2.2	
11	2172	66	3.0	
82	1570	280	17.8	Season 1923
82	2453	467	19.11	Season 1924
26	767	615	80.0	

Hand crossing of Timothy was attempted, but with little success, as on reducing the number of flowers the panicle "dried out".

In order to obtain a cross between self-sterile and fertile plants, a panicle of plant 26 (80% self fertile) was enclosed in a bag with one of plant 32 2.2% self-fertile). A quantity of seed was saved from the panicle of 32 (self-sterile). These were grown and the results are given below.

TABLE/

TABLE XXXI.

SELF-POLLINATION of PROGENY of
Cb 32 (2.2% self fertile) x Cb 26 (80% self fertile)

PLANT NO.	No.of FLOWERS	No.of SEEDS	PERCENTAGE	DATE
94(6)	111	32	28.8	9/7
(21)	107	28	26.2	13/8
(2)	115	16	14.0	9/7
(8)	78	8	10.3	"
(5)	103	7	6.8	"
(3)	112	6	5.4	"
(22)	109	4	3.7	13/8
(28)	110	4	3.6	"
(9)	119	4	3.4	9/7
(1)	124	4	3.2	"
(10)	108	3	2.8	"
(16)	113	3	2.7	"
(26)	117	3	2.6	13/8
(4)	105	2	1.9	9/7
(19)	114	2	1.8	"
(24)	120	2	1.7	13/8
(20)	92	1	1.1	9/7
(23)	102	1	1.0	13/8
(25)	102	1	1.0	"
(13)	104	1	1.0	9/7
(7)	111	1	0.9	"
(27)	96	0 (1 seed on panicle)	0.0	13/8
(15)	118	0	" 0.0	9/7
(18)	103	0	0.0	"

NOTE: The figures given above are the counts from ½" lengths taken from the centre of each panicle.

The percentages of fertile flowers, when panicles of Timothy were freely exposed, were extremely high.

TABLE/

TABLE XXXII.

NATURAL SEEDING.

PLANT NO.	No.of FLOWERS	No.of SEEDS	% FLOWERS Setting SEED.
IV	1702	1657	97.4
	1504	1459	97.0
	1416	1348	95.2
82	1107	1037	94.0
VII	2104	1937	91.3
V	645	581	90.1
	802	703	87.7
	669	561	83.9
VI	1148	987	86.0
	1110	867	78.1

PHLEUM ALPINUM.

TABLE XXXIII.

SELF-POLLINATION.

PLANT	No.of FLOWERS	No.of SEEDS	% FLOWERS Setting SEED.
1	233	196	84.1
2	194	158	81.4
3	174	125	71.1
"*	206	164	79.4
4	193	137	71.0
5	203	123	60.6

* Natural seed ex exposed panicle.

Five plants of P. alpinum which were collected from a wild population in Glen Shee in the Autumn of 1924 were selfed in the greenhouse during last summer. The self fertility percentages for the five plants were high, and are given in TableXXXIII.

COCKSFOOT.

ORDER OF FLOWERING.

The panicle consists of bunches of 3-5 flowered spikelets. The flowers on the upper branches of the panicle are the first to open. In the spikelet flowering commences with the basal flowers (1) and continues upwards; the following is an example:-

14 June	11.40 a.m.	1 opening
15 June	9.5 "	2 opening
18 June	2.45 p.m.	3 open
21 June	9.20 a.m.	4 opening

The period required for a panicle to complete flowering was, under greenhouse conditions, from 14 to 25 days, largely depending on the size of the panicle and atmospheric conditions during the period. For the last few days of the period only occasional flowers opened.

DAILY FLOWERING PERIOD.

Flowering usually started before 10 a.m. and in several instances before 9 a.m. Shortly after the opening of the first flowers the great majority of the day's flowering took place, only occasional flowers opening throughout the afternoon.

Atmospheric conditions have a marked influence/

influence on the times and amount of flowering each day, more so than in ryegrasses. Temperature is not the only factor, for no flowering took place on any plant under observation on 20th June although the temperature for that day reached 90° F.

OPENING OF FLOWERS (ONLY THREE PLANTS UNDER OBSERVATION)

Observations were made over a period of about two weeks during which time all three plants were in full flower.

The period between the opening of the flowers and dehiscence of anthers was found to be variable. The variation to a certain extent at least is due to differences in the behaviour of individual flowers and is not solely caused by external conditions, for, when several flowers on the same panicle open at the same time, the intervals between opening and dehiscence are not identical. But the larger daily differences undoubtedly are caused by an alteration in atmospheric conditions. On the average the interval between the opening of flowers and dehiscence of their anthers was considerably longer than was the case in ryegrasses. The shortest time noted was 10 minutes, and the longest 150 minutes, the average being/

being 61 minutes. In some instances the flowers actually closed before their anthers dehisced.

CLOSING OF FLOWERS.

The majority of freely exposed flowers closed about 3½ hours after opening. The shortest time observed was 90 minutes.

EMASCULATION.

When preparing a panicle of Cocksfoot for emasculation, the removal of many spikelets was necessary. This removal can only be carried out within limits, as "drying out" of the panicle follows too drastic cutting. It was usually necessary to remove one or more complete branches. From the remaining branches whole clusters of spikelets were removed and many spikelets from other clusters. All flowers except 2 per spikelet can be removed with advantage. If emasculated complete spikelets were cross pollinated, the upper flowers set few or no seeds, owing in part probably to their having been damaged at the time of emasculation.

SELF-POLLINATION.

Self-fertilisation varied greatly in individual plants. This variation ranged from complete self-sterility/

self-sterility to a degree of fertility little below that obtained for normal free pollination.

Examples are given in Table XXXIV.

TABLE XXXIV.

PLANT	No.of FLOWERS	No.of SEEDS	% FLOWERS Setting SEED
54	740	0	0
IX	563	152	27
III	872	543	62

The standard with which to compare these results may be taken as 80%, i.e. the percentage of flowers on entire panicles, which set seed under favourable natural conditions.

Unfortunately, cocksfoot is not an ideal species for the study of self-sterility owing to practical difficulties. The determination of flowers containing seeds involves certain difficulties and a very considerable amount of work, as the terminal flowers are small and hard, the flowering glumes being keeled. On a small scale the difficulty might be overcome by reduction of spikelets on the panicle and flowers on the spikelets, but, if this were done, the experimental error would probably be as large, through/

through "drying out" of certain flowers owing to this severe handling.

SELF STERILITY IN A CLONE.

A plant (Cc8) was divided into 36 pieces during the summer of 1923. In the early spring of 1924 these were planted in a bed, isolated as far as possible from other plants of Cocksfoot. These pieces were in full flower on the 24th June. Five panicles were then marked, and, when ripe, the percentage of flowers setting seed was calculated. The figures were :

4427 flowers 367 seeds = 8%.

The percentage obtained when single panicles of this clone were completely isolated in the greenhouse was 5.8%.

FESCUES.

Some observations were made on the following agricultural fescues - Hard Fescue, Red Fescue (Chewing's), Sheeps Fescue and Meadow Fescue, primarily in order to determine if self-sterility occurred in these species. As a result of the investigations, with/

with a very limited number of plants, it is shown that self-sterility, or partial self-fertility, occurs. Whether certain plants reach a figure approaching complete self-fertility it is impossible to say at present. A few of the plants of the different species were divided and these pieces were subjected to different conditions (Cool house and Outside). Certain pieces of the various plants were kept in the greenhouse during the winter. In the summer these were crossed in the greenhouse with pieces of the same plant which had passed the winter outside. Crossing was performed by the enclosing of a panicle of each piece in the same bag (it may be stated that this method of crossing when carried out with panicles of distinct plants gave good results). As a result the percentages of flowers setting seed was not increased.

The following table gives some of the results of selfing for the different species.

TABLE/

TABLE XXXV.

SELF-POLLINATION.

PLANT	DATE of ENCLOSING	CONDI-TIONS	No.of FLS.	No.of SEEDS	% FLOWERS SETTING SEED.	
Hard Fescues						
1	17/5	H.	153	1	0.7	
1	26/5	H.	128	0	0.0	
1	9/6	H.	135	1	0.7	
1	17/5	0	136	0	0.0	
1	17/5	H	123	0	0.0	2 Panicles enclosed together. 1. kept in House during Winter.
1(A)			127	1	0.8	1(A). kept outside " "
1	17/5	0	174	0	0.0	2 Panicles enclosed together.
1(A)			175	0	0.0	1. kept in House during Winter. 1(A) kept outside " "
11	17/5	H	164	0	0.0	
11	17/5	0	143	0	0.0	
Percentage range of 10 plants from 0% to 1.6 %						
Red Fescue						
1	26/5	H	344	26	7.6	
1	5/6	0	558	10	1.8	
11	26/5	H	380	5	1.3	
11	7/6	H	269	2	0.7	
11	5/6	0	448	2	0.5	
Percentage range of 5 plants from 0% to 7.6%						
Sheeps Fescue						
1	5/6	H	222	0	0.0	
1	7/6	H	191	0	0.0	
1	5/6	0	125	0	0.0	
1	5/6	0	165	0	0.0	
11	27/5	H	175	1	0.6	
11	27/5	H	102	2	2.0	
11	27/5	0	93	1	1.1	
11	27/5	0	96	1	1.0	
Percentage range of 10 plants from 0% to 2.7%						
Meadow Fescue						
1	1/7	0	351	9	2.6	
11	22/7	0	384	0	0	
Only two plants tested.						

H. = Cool House

O. = Outside.

NOTE:- The flowers on panicles of Red Fescue were not directly counted. Each spikelet was counted and an estimate of the number of flowers per spikelet made.

ANTHOXANTHUM PUELLII.

Although apparently of no agricultural importance, the fact that plants of this annual species differed from any others worked with, as regards exposure of stigmas, makes the following experiments of some interest.

SELF-FERTILITY.

Under control all plants experimented with readily produced selfed seed.

CONTROLLED CROSS-POLLINATION.

In this species every stigma on a panicle is exposed before the first anthers of that panicle dehisce; those at the apex being fully developed, while those towards the base are just visible.

After exsertion of the anthers an interval of/

of from 5 to 30 minutes elapses before dehiscence. In order to determine at what time the stigmas were receptive before dehiscence of the anthers the flowers on the upper half of a panicle - (those on the lower portion having been removed) - were cross pollinated by hand when the stigmas of the lowest flowers began to protrude. (The flowers were emasculated and bagged at the time the stigmas of the terminal flowers began to appear). When the pollinated flowers were later examined it was found that almost every one had set seed. The experiment was repeated with another panicle on the same plant. In this case every pollinated flower set seed. A complete emasculated panicle on another plant was cross pollinated by hand slightly before the time the anthers of the apical flowers would have dehisced under normal circumstances, (the stigmas of the basal flowers not yet having made their appearance). Every pollinated flower, including the basal ones, except two, set seed. (Those flowers in which the stigmas were not visible at the time of pollination were not pollinated). The average time taken by a complete panicle to flower was 8 days. Therefore the stigmas which were just visible on the lowest flowers at the time of pollination were probably/

probably receptive about 8 days before their anthers would have dehisced under normal conditions. The time pollen remained viable after dehiscence was not ascertained for this species. It is, therefore, impossible to state the exact time at which fertilisation took place. But it is clearly seen that cross fertilisation is more likely to occur than self fertilisation in a population growing under natural conditions, although the individual plants of the population are highly self fertile.

FOXTAIL.

ALOPECURUS PRATENSIS and A. GENICULATUS.

ALOPECURUS PRATENSIS.

In these two species the stigmas are exposed some days previous to anther dehiscence. Five plants of A. pratensis were selfed autonomously under pergamine isolation. Two of these plants were also crossed by hand. A panicle on plant No.(2) (Table XXXVI) was crossed three days before the appearance of the first anthers. At this time many stigmas on the upper portion of the panicle were exposed, while there were only a few on the lower portion. The results/

results show that the stigmas were receptive, as 83.6% of the flowers on the upper portion set seed. It is seen from Table XXXVI that all the five plants tested were more or less self-sterile. FRUWIRTH (1921), however, states that the stigmas are shrivelled at the time of anther dehiscence; but FRANDSEN has found forms in which the stigmas are still fresh at this time, and this agrees with the observations made by the present writer.

TABLE XXXVI.

ALOPECURUS PRATENSIS.

No.of PLANT	DATE	No.of FLS.	No.of SEEDS	% SEEDS	NOTES
1	28/5	91	0	0.0	Selfed
"	"	161	86	53.4	Crossed
2	"	156	2	1.3	Selfed
"	"	155	86	55.5	Crossed and enclosed 3 days before appearance of anthers
					FLS. SEEDS. %
		Upper portion of panicle			61 51 83.6
		Middle " " "			35 21 60.0
		Lower " " "			59 14 23.7
3	"	149	0	0.0	Selfed
4	"	264	1	0.3	"
5	"	111	0	0.0	"
"	"	153	1	0.7	"
"	approx. 28/5	109	1	0.9	
"	"	179	2	1.1	

ALOPECURUS GENICULATUS.

Three plants of A. geniculatus were selfed and as a control other panicles were hand crossed. All three plants were found to be self-fertile. The results are given in Table XXXVII.

TABLE XXXVII.

ALOPECURUS GENICULATUS.

No.of PLANT	DATE	No.of FLS.	No.of SEEDS	% SEEDS	NOTES
1	29/5	175	136	77.7	Hand Crossed
1	28/5	167	146	87.4	Selfed
2	29/5	172	126	79.2	Selfed
2	28/5	132	119	90.2	Crossed (Hand)
3	29/5	261	160	61.3	Selfed
3	28/5	211	128	60.7	Crossed (Hand)

FRUWIRTH (1921) mentions that A. geniculatus x A. pratensis gave a sterile progeny. This is unfortunate, as the two species would have formed excellent material for the study of the inheritance of self-sterility.

DISCUSSION/

DISCUSSION.

TIME OF DEHISCENCE.

In the grasses worked with dehiscence of the anthers always took place some time after the opening of the flowers. It is, therefore, seen that even although certain plants are fully self-fertile - e.g. Poa annua - self-fertilisation is not compulsory. In certain grasses, however, the anthers

(1) dehisce before the opening of the flower, and

(2) dehisce before they are fully exserted.

(1) Barley is a good example of plants in which the anthers dehisce before the opening of the flowers. "In many two rowed barleys the spike remains enclosed in the leaf sheath till after fertilisation and never does entirely emerge". (Carleton 1920)

(2) Example Lolium temulentum (Jenkin 1924)

PERIOD DURING WHICH THE STIGMA REMAINS RECEPTIVE.

The stigmas of the grasses experimented with were found to be receptive for a considerable time both before and after the opening of the flowers. When pollen does not reach maturity till the time the flowers/

flowers open, this early receptivity is of no value from the point of view of seed production. It is, however, of very great importance in self fertilised grasses where pollen is dehisced before the opening of the flowers, e.g. Barley, Wheat and Oats. On the other hand, when the stigmas remain receptive after the opening of the flower, the period of effective pollination is increased to several days. This is of great importance both from the practical hybridiser's standpoint and that of seed production under natural conditions. Under natural conditions, when flowering takes place on a very still day, the dispersal of pollen will be slight. In these circumstances, isolated plants would have little chance of being cross pollinated, if their stigmas only remained receptive for one day, but, when stigmas remain receptive for at least 72 hours, (Perennial Ryegrass, Italian Ryegrass, Tall Oat), the chances are that, during that period, weather suitable for the dispersal of pollen will be encountered.

VIABILITY OF POLLEN.

The length of time pollen remains viable after dehiscence of the anthers, in grasses, appears to/

to be short. Individual plants within a species show variation in this respect. This is clearly demonstrated in the Tall Oat grasses T.O.(1) and T.O.(2). The fact that the life of pollen is so short creates certain difficulties for the hybridiser, as it is not always practicable to have intended male and female parents flowering at the same time.

That pollen of rye remains viable for only a short period is demonstrated by OBERMAYER (1916) (Winter Wheat and Winter Rye). He states that after 4-5 hours only occasional grains germinated with slight energy.

SELF-STERILITY.

As the investigations on the pollination of grasses necessitate strict methods of pollen control, it was essential to find methods whereby spikes or panicles could be completely isolated without in any way preventing fertilisation, and at the same time affording no practical difficulties. It was finally decided to use pergamine paper bags for isolation under greenhouse conditions, and specially constructed pollen proof boxes outside.

The following experiments prove the suitability of these methods.

(1)/

(1) Plants which were self-sterile under either bags or boxes continued to be equally self-sterile when allowed to flower exposed, under complete natural isolation, i.e. by time of flowering. The plants so isolated remained sterile only so long as foreign pollen was excluded, seeds being set whenever cross-fertile plants in flower were introduced into the same house.

(2) When spikes or panicles on different self-sterile, but interfertile, plants were enclosed together, the percentage of flowers setting seed equalled that of natural pollination, e.g.

$Cd_2(2)$ enclosed with $Cd_2(5)$

$Cd_2(2)$ 122 flowers, 89 seeds = 73%

$Cd_2(5)$ 203 flowers, 135 seeds = 66%

(3) Avena fatua, a species known to be self-fertile, when enclosed, was found to remain completely self-fertile (97%).

(4) When emasculated spikes or panicles of cross-fertile plants were cross-pollinated by hand and enclosed, percentages reaching 100 were obtained.

In many plant species self-sterility has been found. Truly self sterile plants have their male/

male and female organs fully developed and functional in compatible combinations. An enclosed plant may, however, be self-sterile owing to its anthers containing no viable pollen. This type of self-sterility must on no account be confused with true self-sterility. The literature on the subject of self-sterility indicates that in the majority of plants the "cause" of sterility is the non-fertilisation of the egg cell. In perennial ryegrass from the few observations made by the present writer it appears that some time after the germination of self-pollen on the stigma pollen tube growth is retarded. EAST (1920) and ANDERSON (1924) working with Nicotiana and KNIGHT (1917) working with apples found that, when self-sterile plants were self-pollinated, germination of pollen took place and the pollen tubes grew down the style at a constant rate of speed but not sufficiently rapid to effect fertilisation during the "life" of the ovule. STOUT (1920) found in Eschscholtzia californica a considerable number of poor seeds present both in pods containing few seeds and in empty pods, suggesting that incompatibility may operate after fertilisation producing embryo abortion. But he points out that in feebly self-fertile plants, as a/

a rule, the few seeds that were developed were located in the upper end of the capsules.

In the cases of self-sterility which are definitely "caused" by either slow pollen tube growth or retarded pollen tube growth in the somatic tissue of the style, sterility does not occur after normal sexual fertilisation. But if as may be the case in E. californica self-sterility operates after fertilisation has taken place normally the case is quite different.

RECIPROCAL CROSSES.

EAST and PARK (1917),working with certain species of Nicotiana where self-sterility is "caused" by the slow growth of the pollen tubes, hold that reciprocal crosses always give the same results as regards fertility. Therefore they suggest that, as regards "that part of the constitution of the pollen grains which affects the behaviour of self-sterile plants, all pollen grains produced by each plant are alike. i.e. with reference to self-sterility pollen grains behave as if they were sporophytic; under normal conditions the pollen tubes produced by pollen from any self-sterile plant will not grow in the styles of that plant with a rapidity sufficient to reach/

reach the ovules during the "life" of the flower on account of the likeness of constitution; pollen tubes will grow with a rapidity sufficient to allow fertilisation to occur if the constitutions of the two proposed parental plants differ from each other in any of these essential factors, by reason of a stimulus possibly analagous to that which makes growth more vigorous in first generation hybrids". This view is also held by ANDERSON (1924). However, there are several reported instances of reciprocal crossing in other plants giving dissimilar results. SIRKS (Stout 1920), in the study of cross incompatibilities in Verbascum phoeniceum,has shown that reciprocal crossings between pairs of plants gave all grades of opposite results in immediate fertility. This agrees with STOUT'S (1916) work on chicory. For chicory STOUT (1920) has found no definite evidence that self-fertility is increased as the flowering season advances. In the same paper he states that in Verbascum phoeniceum there was no evidence of "end season" self fertility. If this is true for all plants of this species, the objection that the dissimilar results of reciprocal crosses found by SIRKS were due to the crossings being made when the fertilities of the plants/

plants in question had changed, owing to end season fertility, would be eliminated. CORRENS (1912), (East and Park 1917), when investigating the question of the influence of age of plant on fertility in Cardamine pratensis, made 18 reciprocal crosses. Of these 7 were successful both ways, 5 failed both ways, 4 were rather indefinite but similar, while only one showed a conflicting result (2 failures one way and 3 successes the other). However, in his table 8 (quoted from East and Park 1917), of 53 reciprocals recorded there, 31 gave the same results, 17 gave different results, while 5 were questionable. CRANE (1925) also has obtained different results from reciprocal crosses in plums.

EFFECT OF ENVIRONMENT.

EAST found that in Nicotiana plants which were self-sterile throughout the greater part of the season became more self-fertile towards the end of the season. This phenomenon is named by EAST "pseudo fertility". The suggestion is that under conditions adverse to vegetative growth self-fertility increases and seeds may develop after self-pollination. Now EAST and PARK (1917) suggest that when a fertile mating is made something inherent in the constitution of the/

the pollen grains causes the style tissue to secrete something which accelerates pollen tube growth, but in self-sterile matings there is not this secretion. They suggest that under conditions adverse to vegetative growth a change has taken place in the style tissue that renders this secretion more easily produced. They conclude, p.531, that "self-fertility is a condition determined by the inheritance received, but can develop to its full perfection only under a favourable environment". EAST & PARK (1917) also found that the amount of "end season" fertility differed for different species of Nicotiana. They conclude, p.533, "that N. Forgetiana (and N. angustifolia has yielded similar results) is a self-sterile species of marked stability, which only occasionally (1 in 300?) produces a plant that shows some self-fertility under adverse conditions. N. alata, on the other hand, has proved to be more unstable in its self-sterility; or better, it has proved to have a norm more nearly intermediate between the extremes complete self-sterility and perfect self-fertility". Plants of alata, however, were practically always completely sterile during the early part of the flowering season. p. 601. "The four species, N. Forgetiana/

Forgetiana, N. alata, N. glutinosa and N. angustifolia, breed true to the tendency toward self-sterility. Self-sterility is fully expressed in these species from the beginning to the middle of the flowering season, especially in plants exhibiting the effect of adverse environmental conditions, some self-fertility may be shown. That this phenomenon is simply a non-inherited fluctuation is confirmed in four ways;

(a) the graduated character of the increased fertility as the flowering season wanes,

(b) the return to complete self-sterility at the beginning of the second flowering season,

(c) the sterility of all progeny raised from selfed seed, and

(d) the failure to obtain an increased tendency toward self-fertility after three successive generations had been raised from selfed seed of the most extreme variants".

STOUT (1920) found in Brassica pekinensis that self-incompatibility of a plant or of a family of plants may be changed by a cultural treatment which reduces vegetative vigour. "In a family of this species grown for three generations less than 10% of the total of 326 plants were highly self-compatible and there was no hereditary effect of selection for self-compatibles. When a generation of this family was grown in small plots with decided reduction of vegetative vigour/

vigour, of a total of 1128 plants there were 734 (65%) that were highly self-compatible, and only 22 (less than 2%) were self-incompatible". STOUT(1923 b) states, p.460 - "and for certain perennials there is some evidence of changes from year to year in relation to the age of the plant". So far as the present writer's observations have gone there is no definite evidence of this "pseudo fertility" occurring in the agricultural grasses. Therefore this phenomenon cannot be taken advantage of in the grass breeding work. DARWIN has some interesting observations on the influence of environment on self-sterile plants. He writes (1878 p.330) "Five species of Passiflora and certain individuals of a sixth species have been found to be self-sterile; but slight changes in their condition, such as being grafted on another stock, or a change of temperature, rendered them self fertile", and on p. 344 (1878), "English Eschcholtzia became self-sterile in one generation when grown in Brazil, though it is self-fertile in England - while the Brazilian plants become self-fertile when they are grown in England. Again Abutilon darwinii, which is self-sterile in its native home in Brazil, became moderately self-fertile after one generation in England".

BAUR/

BAUR (1919), working with several species of Antirrhinum, found that A. siculum and a wild Spanish form, A. majus, were fully self-fertile, while A. Ibanyezii, A. molle, A. glutinosum, A. hispanicum and an undetermined Spanish species were fully self-sterile. A. tortuosum, A. latifolium and two wild forms of a Portuguese species, however, were found to be self-sterile during the first year, although they were slightly self-fertile towards the end of the blooming season. But unlike Nicotiana, these species did not regain their self-sterility with the advent of another blooming period, but were very self-fertile the second year.

SELF-STERILITY AND SELF-FERTILITY IN GRASSES.

Among plant species there are great differences as regards self-fertility and self-sterility. For examples of self-fertile species may be taken the sweet-pea and barley, and Nicotiana Forgetiana and the Tiger Lily (Stout 1923 c) as representing the self-sterile. But between these extremes there exist species which show great range in self-fertility, e.g. Timothy (phleum pratense) and such species as Trifolium pratense (Williams 1925) which have a very low range of self-fertility.

In/

In the grasses there are species which are probably self-fertile and others which show a range from self-sterility to more or less complete self-fertility.

It would appear from the investigation of a few British grasses that there is a more or less clear division between the annuals and the perennials in this respect.

Considering the cereals:-
The annuals Barley, Oats and Wheat are known to be self-fertile, while Rye, the cereal most closely approaching a perennial (The following is a quotation from CARLETON 1920 p. 148 "The ancestral species is perennial ..... cultivated rye if left standing a long time in the field will shoot up again)", is variable as regards fertility.

HERIBERT-NILSSON (1916) has shown that in rye populations there are strongly self-sterile, partially self-fertile and self-sterile plants. The most completely examined population of Petkuser rye showed among 73 examined plants, 71 self-sterile, 1 partially self-fertile and 1 self-fertile. HERIBERT-NILSSON holds that the highly self-fertile plants breed true for self-fertility. He has so far found three/

three races of rye which can be characterised as highly self-fertile. On the other hand, he has obtained self-sterile or almost self-sterile races without difficulty. The original parent of a population 224 (p. 21 Table 4) had a self-fertility percentage of 1.9. The self-fertility percentage of the progeny varied between .1% and 2.9% with an average of 1.3%. The parent of another population 228 was 1.3% self-fertile. The nine descendants (228) had a fertility which varied between .3% - 2.8% and was on the average 1.2%.

In populations of rye there were individuals which showed high or fairly high self-fertility percentages. The behaviour of the progeny of such plants as regards their self-fertility percentages was variable. The mother plant of a population 206 had a fairly high self-fertility percentage (14.8%). Five descendants were examined, and were all in an extreme degree self-fertile sterile. Two plants did not set a single seed, and the highest percentage of fertility was 1.1%. The average of all daughter plants was .5%.

HERIBERT-NILSSON has, therefore, shown that fully self-fertile and self-sterile races can be isolated from rye populations, but whether races with intermediate/

intermediate fertility can be obtained he is not certain, as not sufficient work on the subject has as yet been carried out.

Barley - CARLETON (1920 p. 9) states:-
"In all barleys cross-fertilisation is rare and in many two rowed varieties apparently impossible".

Cultivated Oats and Wheat - CARLETON (1920 p.9) states:-
"Wheat and Oat varieties are usually self-fertilised, but there are adaptions for cross fertilisation, and no doubt the latter occurs much more frequently than is generally supposed. It is certain there are numerous natural crosses among durum wheats and emmers".

In some seasons natural wheat hybrids are more common than in others. OBERMAYER (1916) found that certain individual flowers on wheat spikes were male sterile at the end of the season, although the female organs were fully developed. The glumes of such flowers remained open. This male sterility may perhaps account for some at least of the natural wheat hybrids.

The Wild Wheat of Palestine (discovered by Aaronshon 1906) behaves rather differently as regards pollination to the cultivated varieties. COULTER (1920) p. 192, writes:-
"Perhaps the most notable biological feature of this Palestine wheat in contrast with the domesticated

races/

races is the fact that it is cross-pollinated ..... this wild wheat pushes out its stamens freely and the pollen is scattered by the wind ..... This wild wheat also matures grains through self-pollination, so either method can be used".

From Table XXXVIII it would appear that there is a greater tendency towards full self-fertility in the annual grasses than in the perennials, but it is quite possible that there are individuals among the self-fertile annuals which are more or less self-sterile, just as there are individuals in the more or less self-sterile perennials which are self-fertile.

TABLE XXXVIII.

MODE of POLLINATION in a few BRITISH AGRICULTURAL and other GRASSES.

PERENNIALS

SPECIES	SELF-FERTILITY	TIME of DEHISCENCE of ANTHERS	MODE of FERTILISATION in NATURE
Lolium Perenne	Low Self-Fertility	After opening of Flower	Cross usually compulsory
Lolium italicum	"	"	"
Festuca - (Meadow & Hard)	"	"	"
Arrhenatherum avenaceum, Beauv.	"	"	"

TABLE XXXVIII. (cont.)

SPECIES	SELF-FERTILITY	TIME of DEHISCENCE of ANTHERS	MODE of FERTILISATION in NATURE
Arrhenatherum Avenaceum Beauv.	Low self-fertility	After opening of Flower	Cross usually compulsory
Avena flavescens	"	"	"
Cynosurus cristatus	"	"	" 3 plants tested
Alopecurus pratensis	"	Stigmas exposed several days before dehiscence of Anthers	" 5 plants tested
Dactylis glomerata	Variable	After opening of flower	Cross in some plants compulsory In those approaching complete self fertility optional. Depending on isolation.
Phleum pratense	"	"	"
Phleum alpinum	Self-fertile	"	Cross or self 5 plants tested
Poa nemoralis (Frandsen 1917)	"	-	-

TABLE XXXVIII. (cont.)

ANNUALS

SPECIES	SELF-FERTILITY	TIME of DEHISCENCE of ANTHERS	MODE of FERTILISATION in NATURE
Cultivated Barley (Carleton 1920)	Self-fertile	Before opening of flowers	Self compulsory in many two-rowed varieties
Cultivated Oats (Carleton 1920)	"	"	Self
Avena fatua	"	"	"
Cultivated Wheat (Carleton 1920)	"	"	"
Palestine Wild Wheat (Coulter 1920)	"	-	Cross
Rye (Heribert-Nilsson 1920)	Low self-fertility	After opening of flowers	Cross - in many cases compulsory
Lolium temulentum (Jenkin 1924)	Self-fertile	At time of opening of flowers	
Bromus arvensis (Frandsen 1917)	"	-	-

TABLE XXXVIII (cont.)

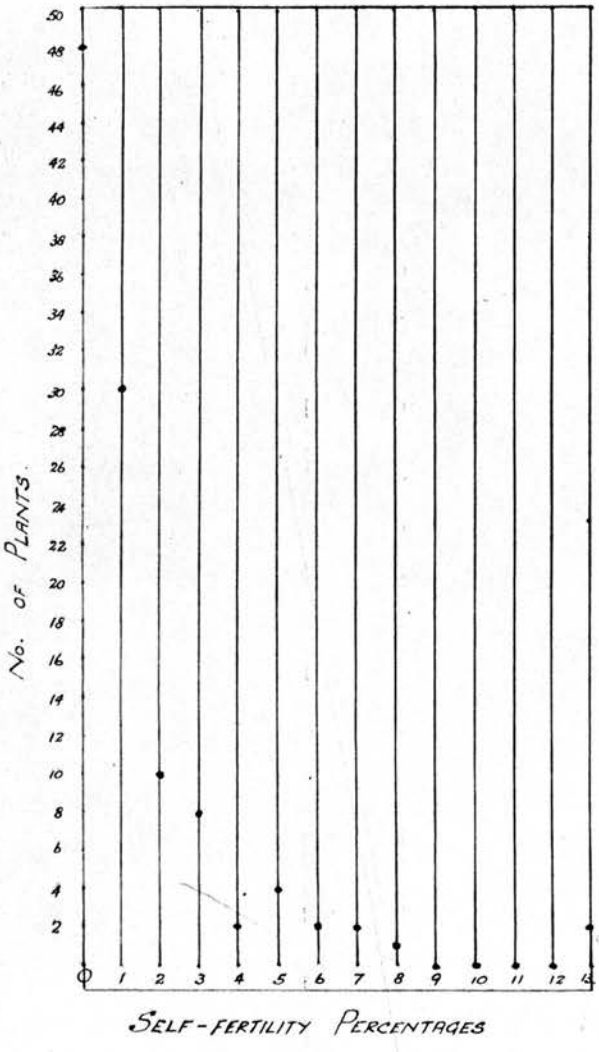
SPECIES	SELF-FERTILITY	TIME of DEHISCENCE of ANTHERS	MODE of FERTILISATION in NATURE
Alopecurus geniculatus	Self-fertile	Stigmas exposed several days before dehiscence of anthers	Cross
Anthoxanthum Puellii Lec. & Lam.	"	"	"
Poa annua	"	After opening of flowers	Cross probable
Agropyron caninum (Malte 1921)	"	-	

(a)

Table XXXIX on page 107 gives the frequency distribution of the self-fertility percentages for a population of related plants of Perennial Ryegrass. It will be seen that the self-fertility percentage range is from 0% to 12.6% and that the greater proportion of individuals are towards the lower percentages. The original two parents of this family had self-fertility/

TABLE XXXIX

FREQUENCY DISTRIBUTION - SELF-FERTILITY PERCENTAGES FOR 109 RELATED PLANTS.



fertility percentages of .6% and 4.6%. There was no definite evidence of "mid" or "end season" fertility for either parent and further, one parent remained more or less constant at 4.6% for three successive years. The selfing of the progeny of this cross was carried out during the first flowering period of each plant, and those plants which were selfed at intervals throughout the season gave no definite indication of variation in their self-fertility percentages. The results, as far as the frequency distribution of the self-fertility percentages is concerned, are very similar to those found by STOUT (1920) working with the variety red-leaved Treviso of Chichorium Intybus. The variety red-leaved Treviso was kept in culture for the first three years (1914, 1915, 1916) by crossing self-incompatible plants. In 1915 a very feebly self-fertile plant was obtained. Among the 1916 crop grown from self-incompatible parentage there were 11 plants which were self-fertile to some degree, and of those 4 were highly self-fertile. Three lines were grown in the I_1 and two families were continued into the I_2. The parents of the 3 lines in the I_1 had self-fertility percentages of 56%, 55% and 70%. The selfed populations raised from these plants had a very considerable/

considerable range of self-fertility, 0% to 60%, the frequencies being greatest towards self-sterility, diminishing towards 60%. A very similar range was obtained in the I_2, but both the proportion of plants that were self-fertile and the range of self-fertility (0% - 75%) were increased in the I_2. The ranges as pointed out by STOUT were not due to a mingling of data collected at early and late periods of bloom.

CONCLUSIONS.

From the perusal of all the evidence given above it is extremely difficult to come to any definite conclusions with regard to self-sterility in plants when true functional sterility does not occur. But it is evident that at least differences occur between different plant groups, so that the data collected from any one species or variety are not necessarily applicable to another species or variety. Again, environment appears to exert a strong influence on the behaviour of some self sterile plants. From the work of the various investigators it is clear that they came to a more or less definite conclusion that self-sterility has a genetic basis.

The following are the interesting conclusions of STOUT, who has done a very considerable amount of work/

work on this subject. He concludes (Stout 1920) that "In hermaphrodites incompatibilities have arisen in species, and evidently are arising at the present time, through fluctuating variation in the physiological differentiation of the sex organs. These phenomena run parallel to the anatomical variations leading to intersexualism and dioecism.

"The evidence supporting this general conclusion from my own studies and from the facts revealed by other recent studies as well may here be summarised under the following heads:-

"(1) The indisputable evidence that compatibility and incompatibility in many species are highly variable both in expression and in heredity.

(2) The evidence is conclusive that self-incompatibility is not always, if ever, induced by self-fertilisation and inbreeding.

(3) Variations, now recognised as phenomena of intersexualism in morphological sex differentiation in species which are prevailingly hermaphrodite or dioecious, are quite analogous to variations in physiological/

physiological differentiation.

(4) The obvious conclusion is that sex differentiation and determination, and hence compatibility and incompatibility in hermaphrodites are fundamentally of ontogenetic and biogenetic development."

With regard to (4) he goes on to say:- "A self-incompatible plant is itself the result of a compatible fertilisation. Cytoplasmic and nuclear elements of an egg and a sperm fuse to form a zygote highly vigorous and of high sexual potentiality, yet its sex organs fail to function together. The elements which were compatible in the fertilisation and in the life of the resulting zygote become incompatible during ontogeny. Yet the incompatibility does not arise simply because of the element of constitutional similarityinvolved in hermaphroditism, nor because of sex differentiation as such, for a sister plant with the same parentage and ancestry may be highly self-compatible.

Sexuality is a cyclic recurring condition which makes possible the fusion of cells and nucleii and the pairing of chromosomes. The incompatibilities exhibited in processes of fertilisation are due to physiological/

physiological properties that are acquired during sex differentiation."

These conclusions of STOUT tend towards an hypothesis of a balance of conflicting physiological factors similar to the suggestion given by GOLDSCHMIDT for the facts for the Gypsy Moth (Lymantria). GOLDSCHMIDT'S experiments were concerned with L. dispar and L. japonica. He has shown that, with proper combinations of different races of these two species, intersexes may be produced which occupy all possible intermediate positions in a continuous series in which maleness and femaleness are the two extremes. Thus zygotic females may range in character from the normal female to individuals almost resembling the male.

Now as regards self-sterility:-

It is possible that the pollen tube and stigma interaction, developed under the influence of the environment of the physiological factors determining self-sterility and self-fertility, depends on the balance attained between the conflicting potencies. From this it can be seen that, when the balance of potencies favoured self-fertility, some degree of self-fertility would be evident. It is also possible that the environment may not remain stable throughout the/

the entire flowering season, giving rise to such phenomena as mid- and end-season fertility. The effect of environment on the determination of sex is illustrated by the following experiments. MRS TREAT (1873) found that, if caterpillars were starved before entering the chrysalis, they gave rise to a preponderance of male imagoes, while conversely, those of the same brood that were highly fed produced excess of females. YUNG (1881) reached the same result in the case of Amphibia; highly fed tadpoles producing a great excess of females, and under fed ones an excess of males.

CROSS STERILITY.

It has been found by investigators, working with self sterile populations, that a population can be divided by means of its cross sterility relationships into a number of inter-fertile intra-sterile classes. EAST & PARK (1917) and ANDERSON (1924), working on cross-sterility in the genus Nicotiana, found that individuals arising from a cross could be divided/

divided by means of their cross-sterility relationships into a number of inter-fertile intra-sterile classes. ANDERSON (1924) in addition to establishing the relation between the classes of individual families has shown that relations exist between the classes of different families. If crosses between two classes in different families were repeatedly sterile, he assumes that the two classes were identical.

In addition to the fact that inter-fertile intra-sterile classes exist in Nicotiana, they have been found in other plant groups by the following workers.

CORRENS, working with 13 plants of the F_1 from a cross between two plants of Linaria vulgaris, found 4 classes all inter-fertile and intra-sterile with the exception of Class II, which were fertile with Class B when used as a male parent and sterile when used as a female.

When CORRENS (Baur 1919 p. 187) crossed plants of Cardamine, 4 classes of plants were obtained. One class was sterile with both parents, one sterile with one parent, one sterile with the other parent, and the fourth class fertile with both parents. BAUR (1919 a) (Anderson 1924) found that a population resulting/

resulting from a cross between two self-sterile plants of Antirrhinum hispanicum could be divided by their cross-sterility relationships into two inter-fertile, intra-sterile groups of approximately equal size. One group was fertile with both parents, one sterile with one, but fertile with the other. LEHMANN (1919) working with the self-sterile species Veronica syriaca found inter-fertile, intra-sterile groups; as did SHULL (1923) in his populations of the self-sterile species Bursa grandiflora (Bois). CRANE (1925) working with plums, finds 4 groups of incompatibles.

There is evidence that cross sterility, like self-sterility, has a genetic basis. EAST & PARK (1917) hold that, when two self-sterile species differing by a large number of hereditary factors are crossed, a high degree of cross-fertility in the F_1 and F_2 generations will be evident, with a subsequent increase of cross-sterility in later generations produced by the closest possible inbreeding. Plants would appear similar for the factors affecting cross-fertility and these should be cross-sterile. The F_2 generation of a cross between N. Forgetiana and N. alata showed a low percentage of cross-sterility (2.4%). The cross was followed to the F5 generation by/

by means of successive sib mating. The F_3 gave a cross-sterility percentage of 6%, the F_4 9%, while the F_5 generation showed 21.7% cross sterility. The smaller the number of factors affecting cross-sterility the smaller will be the number of intra-sterile inter-fertile classes after a period of inbreeding.

"The most important new fact discovered in Nicotiana alata is the probability that a population may exist consisting of only one intra-sterile class".

ANDERSON (1924) found in Nicotiana (1) "that nearly related families possessed certain classes in common, while the classes of more distantly related families were all distinct from one another". (2) The same classes appeared in successive generations.

WILLIAMS (1925) has shown that cross-sterility occurs in Trifolium pratense, a practically self-sterile species. When F_1 plants were intercrossed, the cross-fertility percentages were considerably lower than the cross-fertility percentages by the crossing of the parents. The cross-fertility of the parents of one family was 61.8%, while the cross-fertility of four F_1 brother and sister crosses ranged from 45.9% to 0.2%. In another family the

cross/

cross-fertility of the parent plants was 77.6%, while two F_1 plants were much more cross-fertile when pollinated with pollen from unrelated plants. In another table he gives the cross fertility percentages for five F_2 plants of one family. Four of the F_2 crosses were completely sterile, while the fifth cross only produced 6.4% seeds (This F_2 family was obtained by intercrossing two F_1 plants which gave a cross fertility of 66.6%). He states that in this family there were distinct signs of reduced vegetative vigour. Unfortunately, however, there is no mention of experiments having been carried out with a view to determine whether true functional sterility was present.

From the small amount of data obtained from the experiments with perennial ryegrass by the present writer, it would appear that families 298 and 302 had at least one intra-sterile class in common, since both contained an individual which was cross-sterile with plant 134, although their female organs were proved to be functional, and when these two individuals were themselves crossed, no seeds were set. In the family 298 there were two plants which were inter-sterile but completely cross-fertile with plant 134; presumably/

presumably, therefore, these plants belong to the same class, but do not belong to the class represented by the individuals mentioned above.

134 x 41
1

1 1
142(a) x 134 142(b) x 134
1 1
1 1
Population 298 Population 302

Since all the crosses were made as nearly as possible about the same date, and were not repeated at intervals throughout the flowering season, no data were obtained regarding "pseudo cross-fertility". EAST, however, has recorded the presence of "pseudo corss-fertility" in the genus Nicotiana.

CONCLUSIONS.

As already suggested, self-sterility and fertility are governed by a balance of potencies. It is possible that cross-fertility and cross-sterility are controlled in a similar manner; but it is quite possible that the factors determining cross-fertility and cross-sterility are not the same as those determining self-fertility and self-sterility. Now, as the great bulk of evidence goes to show that pairs of reciprocals give like results, either when fertile/

fertile or sterile, EAST & PARK assume that the pollen grains carry the characteristics, with regard to these fertility factors, of the sporophyte.

Since the behaviour of pollen tubes is similar in both self-sterile and cross-sterile matings, the "cause" of sterility in both cases is the same. Therefore we are dealing with the pollen grains and the stigma, not the pollen grains and the ovules. Without the assumption that the pollen grains carry sporophytic characteristics similar results in reciprocal crosses can occur; for in reciprocal matings between a plant A and a plant B all pollen grains in the haploid condition of the plant B would interact with the stigma, in the diploid condition of plant B. The reciprocal would involve the interaction of all the pollen grains of B and the stigma of A. Theoretically the reciprocal matings would only be absolutely identical in certain cases, but in practice the differences in fertilities would be detected only with difficulty.

MALE STERILITY.

A few plants of perennial ryegrass have been found which produced little or no pollen. The anthers were found to be shrivelled, and only on occasional/

occasional flowers was there a small amount of pollen available. These plants, however, behaved as functional females. This male-sterility in perennial ryegrass is probably an inherited condition. Several investigators working on the subject have proved this to be the case in other plant species.

FEMALE STERILITY.

WITTE (1919) found the presence of female sterility in a Swedish race of Timothy (phleum pratense). The female sterile plants were first discovered in 1914 by the fact that they produced no seeds even when freely exposed. These individuals were observed in the years 1915 - 1918 and behaved in a similar manner. On examination it was found that sterility was due to the malformation of the gynaecium; the stamens and the pollen sac were, however, quite normal. From WITTE'S results female sterility in timothy appears to have a genetic basis.

BREEDING.

We now come to the problem of the improvement of the Agricultural Grasses; but, before considering the methods applicable to plants under strict control, it is advisable to enquire into the manner of/

of seed production on a commercial basis. From my work of the examination of individual plants in cultivated populations of both perennial ryegrass and cocksfoot, it is evident that within a single strain great variation exists, both as regards morphological and physiological characters. A typical example of the variation occurring between individual plants in a strain of perennial ryegrass is given in Table XL.

TABLE/

TABLE XL.

PLANT NO.	No.of SPIKES Visible	No.of SPIKES Total	TOTAL Wt. of 5 INCHES in GMS.	WEIGHT of STEM in 5 INCHES	WEIGHT of LEAVES in 5 INCHES	% of TOTAL WEIGHT LEAVES	REMARKS
185(2)	18	31	13.75	7.65	6.10	44	
(3)	16	19	10.57	4.98	5.59	54	
(4)	23	29	9.18	6.46	2.72	30	
(1)	8	8	.96	.81	.15	16	very early
186(4)	20	30	18.20	7.49	10.71	59	
(2)	23	26	13.94	7.11	6.83	48	
(3)	15	18	3.22	2.75	.47	15	
(1)	4	4	.75	.54	.21	28	very early
190(4)	25	52	20.18	13.12	7.06	35	
(1)	10	12	4.04	1.92	2.12	52	
(2)	8	10	2.18	1.29	.89	41	
(3)	10	10	1.28	1.13	.15	12	very early
194(3)	30	43	22.78	11.18	11.60	51	
(2)	10	11	6.06	2.36	3.70	61	
(1)	8	9	2.50	1.45	1.05	42	
(4)	11	13	1.90	1.45	.45	24	early
214(3)	10	13	3.77	2.25	1.52	40	
(2)	11	13	3.52	2.30	1.22	34	
(4)	8	8	.84	.80	.04	5	very early
(1)	6	6	.83	.73	.10	12	very early
232(3)	12	13	6.64	2.79	3.85	58	
(4)	11	14	5.60	2.40	3.20	57	
(2)	13	15	2.42	2.03	.39	16	
(1)	13	14	1.15	.98	.17	15	

NOTE: Method of Cutting.

Plants brought upright by hand and tied into a bunch. Cut over 4 in. above ground surface. The number of visible spikes was counted and the bunch cut again 5 in. above previous cut. The weights of these 5 in. lengths are shown in the table.

METHOD OF SEPARATING LEAVES FROM STEMS.

Flowering stems and "fertile" shoots (shoots containing an immature spike) after removal of leaf blades were weighed as stems. Leaves plus "sterile" shoots (shoots containing no spike) were weighed as leaves.

The number of "fertile" shoots per plant was counted and added to the number of visible shoots; the sum is entered in the total column under No. of spikes.

The data for the above table were obtained from an experiment in which spikes from a large number of different plants in a population were collected. Six seeds from each spike were sown in sterilised soil. When the seedlings were about 1" in height they were transplanted into long narrow boxes, one box being allowed to each lot of seedlings from a single spike. At the time of cutting the two plants occupying/

occupying the end positions of each box were discarded. The table gives the figures obtained for six boxes in which no deaths had occurred. Since all the plants were grown under as nearly identical conditions as possible, the differences between the plants cannot be, to any extent, considered as fluctuations, but rather they represent the inherited response of the plants to a given environment. On referring to the table, it will be seen that those plants indicated as "early" have a very low total weight of herbage. Their inherited tendency seems to be the rapid production of seeds at the expense of leaves.

But after the study of strains as a whole, instead of individual plants within strains, there is no doubt that differences between strains of a species do exist. These differences as STAPLEDON (1924) points out, are not generally due to controlled breeding or to the exercise of any precautions designed to safeguard purity, but to the conditions under which the species are grown for seed in different parts of the world. It is conceivable that seed grown in exceptionally dry districts will produce a higher proportion of drought resisting plants than seed collected from plants growing in wet districts. It is, therefore/

therefore, a case of natural selection and not selection by man.

The majority of cultivated strains of perennial ryegrass at the present time, however, are remarkably alike as regards the time of year at which flowering commences. The great majority of the plants are early flowering. This condition has no doubt arisen as a result of the methods of seed growing commonly employed. These methods involve a constant process of artificial selection of the types which reach maturity early, and as indicated in Table XL. They are the types which produce the least amount of pasturage. Another disadvantage of the present system is that the seed crops are harvested from first year grass (i.e. the 2nd year from seed). This practice does not allow of the more slowly maturing and presumably more perennial types being represented to any extent in the commercial seed crop.

WILD POPULATIONS.

In addition to the study of cultivated strains (perennial ryegrass) and individual plants within these strains, certain "wild" local populations have been examined. It has been found that individuals in some of these wild populations are remarkably/

remarkably alike as regards certain characters of agricultural importance, and further different local populations exhibit very marked differences in type. That these differences are not simply fluctuations due to differences in environment, but are genetic in nature, is indicated by the fact that, when "wild" local populations were grown under the same conditions at the Plant Breeding Station at Corstorphine, they could be distinguished from each other without difficulty. The study of the effect of the various environmental factors upon the individual plant has received much attention by various writers, but the problem of the hereditary variation of wild plants in relation to habitat has remained experimentally almost unattacked.

Natural selection no doubt plays an important part in determining the general type of a local population. For example, it is possible to find a local population in which the inherited tendency is towards a prostrate habit of growth; and another consisting of more or less erect individuals. It was found that in plants collected from a "wild" coastal population which was subjected to very heavy grazing by both sheep and rabbits, the prostrate habit of growth/

growth was very pronounced. The individuals of the population, although very similar in appearance, were not all of the same genotype, as was proved by the occurrence of erect plants in the progeny of certain pairs of individuals crossed by hand under strict control. It is significant, however, that the majority of crosses between pairs of prostrate plants gave more or less uniform progeny having the flat habit of growth. Now, since all the individuals collected from this population:-

(1) showed the prostrate habit of growth,

(2) when planted out at Corstorphine and allowed to develop naturally (i.e. without grazing or cutting), retained their prostrate habit of growth, and

(3) were not all homozygous prostrates;

it follows that selection of some kind had made the population phenotypically alike.

A possible explanation of the uniformity is as follows:-

That owing to the heavy grazing only certain genotypes which were phenotypically alike could survive or at least set seed. This is borne out by the fact that all the plants from the population were phenotypically prostrate but not necessarily homozygous for this character. It is probable, therefore, that, if the environment can produce a prostrate phenotype from a particular/

particular genotype, that genotype will continue in the population. It does not follow, however, that these genotypes will always produce prostrate plants under all environmental conditions.

Now as regards the origin of such a population:-

It would appear either -

(1) that the plants at the formation of the population were heterozygous for this character, and that as a result of the erects having been suppressed or permitted to produce seed only rarely the possible crosses in the population were between heterozygous prostrate and homozygous prostrate; and assuming that these two types were equally favoured, it follows that as time went on the population more closely approached the homozygous condition; or

(2) that the original plants were homozygous for the prostrate habit and had later been occasionally crossed with erect plants which had flowered under a suitable environment.

The observations so far made on local populations bear out the statement of HAGEDOORN:- "that the variability is most marked in non-essential characters", and that uniformity is only arrived at for the essential characters, which supports the view of natural selection as an important factor in fixing the general type of a population.

If in general there is a tendency for "wild" local populations of the allogamous grasses to become genotypically/

genotypically pure in at least some characters, these populations should form excellent material for future breeding work.

DIFFERENCE BETWEEN CULTIVATED AND WILD TYPES.

Those species of agricultural grasses which are sown with the object of cutting them for seed in the following year have as previously shown developed along well defined lines decidedly unsuitable for pasture purposes. There are in existence, however, strains of perennial ryegrass admirably adapted for hay. At the present time, therefore, attention should be paid more especially to the questions of raising pasture strains of the important agricultural grasses, such as Cocksfoot, Perennial Ryegrass and Timothy.

The cultivated agricultural species must have at one time arisen from the wild species and it has been by combined artificial and natural selection that the present commercial types have been evolved. But from my own observations and those of STAPLEDON (1924 a) a fresh start from the wild species is indicated. The following is an extract from STAPLEDON (1924) "The indigenous tend to flower later than the commercial; the plants are more leafy; produce many more tillers; under a drastic system of cutting the indigenous/

indigenous show a higher power of resistance and a less considerable reduction of tillers; and they are undoubtedly more persistent and long lasting. On the average the indigenous are not so early to start growth in the spring and do not yield such heavy hay crops in the first year. They tend also to be less heavy seed producers than the commercial".

The late flowering habit is of great practical importance, since late flowering plants would tend to extend the grazing period, and as pointed out by GODDEN (1925) nutritive value falls after flowering. The flowering stems are, however, more valuable at the end of the flowering period than at the beginning.

CHRISTOPH (1925). Differences in times of flowering can be utilised as ~~the~~ a method of natural isolation.

As regards leafyness, it is shown by FAGAN and JONES that the leaf portion of the plant is distinctly richer in nutritive material than the stem portion.

Another advantage of the use of "wild" local populations as a basis of breeding work is the fact that in different areas wild populations are subjected to very different climatic conditions, and it should be possible to raise strains specially suited to certain districts by taking advantage of this fact.

BREEDING/

BREEDING METHODS.

Selection and natural isolation are the most prominent points in the literature on grass breeding. The general method of most workers is that of selecting promising plants from existing commercial strains, pastures etc. These are divided and planted in clone plots. The best clones are allowed to seed. The seedlings are grown and planted in plots from which further selection is made. During the sexual multiplication isolation is obtained by separating the flowering plots as far as possible from each other. In self-fertile species self-fertilised seed is obtained by strictly controlled autonomous self-pollination or by the method of separation of clones.

In self-sterile or only partially self-fertile clones the isolation obtained for sexual multiplication by separation cannot be complete under plant breeding station conditions owing to the available space being limited and to the large number of flowering grasses present. It follows, therefore, that many of the seeds formed will be the result of cross-fertilisation with unknown plants. The use of cloth fences and tall growing cereals such as rye has/

has been advocated as a means of insuring more complete isolation of clone plots. The present writer, however, is of the opinion that such methods can only be partially successful, especially when dealing with small clones.

In order to overcome the difficulty of low seed production in self-sterile or partially self-fertile clones ZADE (1918 and 1925) recommends the interplanting of two clones which are similar in appearance and allowing them to seed freely. The tests made by him have shown that among the progeny of some of these groups the selected type had been retained, and he suggests that one would arrive at a fairly constant strain by further selection of the progeny.

At the present time there are several new "pedigree" strains on the market. Several of these have been tested. STAPLEDON (1924 a) remarks:- "Pedigree strains are now procurable from Sweden and Denmark, but the little evidence available does not indicate that they are better adapted to the formation of long duration grass than ordinary commercial seed."

The problem at present, therefore, is that of the production of improved strains of pasture grasses breeding true for at least a few essential characters/

characters. Such plants would also be extremely useful for future genetical work. Attempting to obtain this improvement by promiscuously crossing self-sterile individuals in commercial strains, which have already been widely crossed, is, however, quite futile. An analysis of the material to be used must first be made by systematic breeding. Then the different constant types which may be ultimately obtained can be crossed, and one combination after another can be tested until a real improvement is effected. For this to be realised strictly controlled pollination is required.

Attempts to raise self-fertile lines of the agricultural grasses would be a matter of chance until the self-sterility problem has been further investigated. At present the most suitable method of raising strains true for at least some desirable characters appears to be that of selection from a "wild" local population, in which variation as regards essential characters is at a minimum and the strictly controlled hand crossing of pairs of selected phenotypes similar for the desired character or characters, with subsequent study of their progeny. In this manner the genetic constitution of the original pairs can be determined/

determined. In addition to this genotypic selection, inbreeding of similar desirable phenotypes (i.e. :- brother and sister mating) could be carried out in the F_1 of an original mating. From within each line (F_2) so obtained a similar selection and pairing could be made. Repetition of this method through a number of generations will lead to homozygosity. When plants have attained homozygosity for one desirable character they would be used as material for selection and pairing on the basis of a further character. This process of dealing with only one character at a time is no doubt slow, but appears to be the most suitable method.

The above method overcomes the difficulty of obtaining strictly controlled seed from self-sterile plants especially for plants in which hand crossing is comparatively easily performed.

As regards inbreeding, difficulty in crossing individuals might arise in certain instances owing to cross-sterility. But, if grasses fall into several interfertile, intrasterile classes, as has been observed in other plant groups, the difficulty could be overcome by the crossing of plants belonging to different intrasterile classes.

Whether inbreeding in grasses reduces vigour is/

is doubtful, since little strict inbreeding has been done. ZADE, however, indicates that in some instances at least some reduction of vigour took place. HERIBERT-NILSSON, working with self-fertile races of rye, found that inbreeding did not appear to diminish fertility, but the vitality of the progeny was weakened.

MULTIPLICATION OF STRAINS.

When strains reach such dimensions that isolation becomes impossible under either bags or boxes, other methods are required.

There are areas in Scotland where the important agricultural grasses are not found, and it is in these areas in which natural isolation is insured that multiplication of strains might with advantage be attempted. Experiments in this connection were carried out during the summer of 1925 in the Lammermoor Hills. Two clones of perennial ryegrass (Ca 41, self-fertility .6% and Ca 134 self-fertility 4.6%) were interplanted. Both clones came into flower at the same time. On later examination it was found that practically no seeds were set by clone 41, while 134 gave a setting below that of natural seeding at Corstorphine.

The/

The results indicate that different environmental conditions may have different effects on seed production, since it was found by experiment that both plants were completely inter-fertile at the Plant Breeding Station.

BREEDING.

In general, the "wild" types of the agricultural grasses flower later than the commercial. This forms a natural barrier to cross-fertilisation between the two types. It is possible, however, to control the time of flowering of any of the agricultural grasses by cultural treatment such as cutting or grazing. On a small scale this method of isolation affords few difficulties, but on seed growing farms a serious difficulty arises with regard to the late flowering strains, since both the harvest of the grasses and the cereal harvest would coincide.

PREVENTION OF DETERIORATION IN STRAINS.

If it should prove possible to raise improved strains of the agricultural grasses breeding true for some desirable characters some precautions will be necessary to prevent such strains deteriorating during the process of field multiplication, before/

before being placed on the market. In order to overcome the present difficulty of constant selection of the early maturing plants the strains might be grazed for one or more years before cutting for seed. Further if no isolated locality were available, it would be possible to have natural isolation by taking advantage of late flowering strains. No doubt the suggestions would entail a higher cost of seed production, more especially when it is remembered that in general, indigenous plants produce less seed than the present commercial strains, and that the grass seed and cereal harvest would, no doubt, overlap to some extent.

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SUMMARY/

S U M M A R Y.

1. The presence of self-sterility in the important agricultural grasses has definitely been proved.
2. Some species show a greater range of self-fertility than others.
3. The annual grasses appear to be more self-fertile than the perennial.
4. From the few observations made on the pollen tube growth on self-pollinated stigmas of an almost self-sterile plant of perennial ryegrass self-sterility appears to be due to the pollen tubes not reaching the ovules.
5. From the results of hand crossing of plants within a family of perennial ryegrass the presence of cross-sterility is indicated.
6. Natural isolation in the initial stages of breeding is not sufficient. Strictly controlled methods are necessary. Strictly controlled hand crossing of similar phenotypes within "wild" local populations is indicated for self sterile species, and is feasible.
7. Suitable methods of field multiplication are essential.

Jas. W. Gregor.

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